
THE ARCHITECTURE OF INFLORESCENCES IN THE MYRTALES¹

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In Memory of Dorothea Weberling,
April 25, 1928–February 2, 1988.

ABSTRACT

In the Myrtales a great variety of inflorescences are found. In some families such as Oliniaceae or Alzateaceae (formerly included into Lythraceae) the inflorescences are exclusively of the more primitive monotelic type. In others gradual transitions from the monotelic to the polytelic type can be observed. Within the Lythraceae the genera Lawsonia, Lagerstroemia, and Galpinia and—if included as subfamilies—the Punicoideae and Sonneratioidae still represent the monotelic type, whereas in the majority of the genera polytelic inflorescences are found. These often show a botrytic ramification, although the basic type of ramification is a thyrses. Among the great diversity of forms the gradual specialization of a short shoot–long shoot system can be observed, especially in the genus Ginorea. The same can be seen within the Combretaceae, which are polytelic throughout. As in most Myrtales families, phylloscopic accessory buds or branches are frequently occurring and sometimes form a determining factor for the shape of a flowering plant. In Onagraceae polytelic structure of inflorescences is also manifested throughout the family and inflorescences as botrya or spikes are known. On this basis an impressive diversity exists, especially in the variations of the proportions between the terminal main inflorescence and the extension of the enrichment zone, the number and size of paracladia, the length of the internodes, and the possibility of a reversion of the inflorescence apex to vegetative growth, commonly called proliferation. The latter often occurs in the inflorescences of Myrtaceae in which the “central type” and perhaps the phylogenetically primitive form is a monotelic thyrsoid or a panicle. Even in proliferating or in truncate syninflorescences the monotelic character is evident by the fact that all paracladia, including those with more than one pair of flower-bearing branches, are provided with a terminal flower. The efflorescence of the proliferating inflorescence can be delayed for such a long time that the proliferating shoot may even form branches above the flower-bearing zone. Thus inflorescences of this shape sometimes were regarded as “intercalary inflorescences.” In some cases (some species of Eugenia) the transition to the polytelic type seems to be complete. In the majority of the Penaeaceae the inflorescences forming thyrsoids or stachyoids follow the monotelic type. Some facultatively or constantly truncate syninflorescences form a transition to taxa with polytelic syninflorescences. In Psiloxylaceae the flower-bearing systems are brachyblasts reduced to their botrytic inflorescence and inserted on older axes. Variety of inflorescences in Melastomataceae corresponds to the size of the family but shows less diversity than Myrtaceae. The inflorescences are monotelic. Cases of complete transitions to polytelic structures were not found. Even truncation seems to be rare and only a single case is reported for Medinilla magnifica. On the other hand, proliferation is not rare.

FUNDAMENTAL FEATURES OF INFLORESCENCE MORPHOLOGY

Since differences and conformities in the arrangement of flowers are characteristic for smaller or larger taxonomic groups, these criteria have been used in many ways since the very beginning of systematic botany. For this purpose an elaborate descriptive terminology

is in use designating the different modes of foliation and especially of ramification by well-known terms such as raceme, spike, umbel, panicle, etc. Many efforts have been made to establish a natural system for the immense diversity of inflorescences. The results, however, remained insufficient, primarily because the empirical basis was too small. Above all, it does not follow that the flower-bearing parts

¹ Supported in part by grants from the U.S. National Science Foundation to P. H. Raven, most recently BSR-8518906.

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to which a term such as "spike," "umbel," or "dichasium" is applied are necessarily homologous. For that reason, one cannot achieve correct interpretation of the morphology of inflorescences by focusing exclusively on those flower-bearing ramification systems that by some conspicuous quality appear to be "units." One must also consider the position of these entities within the structural plan of the whole plant. Only in this way it is possible to ascertain which flower-bearing elements may legitimately be compared as identical structures. This, however, is connected with the elucidation of the structural plans of flowering plants and therefore needs a broad empirical basis. According to Troll (in Troll & Weber, 1955; Troll, 1964, 1969), the great diversity of inflorescences is due to the variation of two types only: the polytelic and the monotelic types.

In the *monotelic* inflorescence (Fig. 1 I), the apex of the inflorescence axis commonly ends with a *terminal flower*. This also applies to all the floral branches below the terminal flower. All of these branches, whether branched or not, are homologous elements, and they are all referred to by the term *paracladia* (pc; singular: paracladium), because these branches repeat the structure of the main axis of the flowering system. Accordingly, their ramifications are called paracladia of the second to n^{th} order. The whole area that produces flowering paracladia (Bereicherungstriebe, "enriching branches") may be designated as the *enrichment zone* (Bereicherungszone, "paracladial zone"). In the lower part of the flowering shoot this zone is commonly preceded by an *inhibition zone*, within which the development of paracladia is inhibited more or less abruptly (Figs. 1, 3 I). The same zonation can be recognized in the individual paracladia if these are not reduced in any way. In perennials the axillary buds at the base of the whole stem do not develop within the same season but will give rise to innovation shoots at the beginning of the following season. Therefore, this area has to be distinguished as an *innovation zone*.

In the *polytelic* type of inflorescence (Fig.

1 II), which is no less frequent in angiosperms, there is no terminal flower at the summit of the primary axis. The shoot apex remains *indefinite* after developing a smaller or greater number of lateral flowers, the last of which often do not complete their development but atrophy in the same way as the end of the axis. This apical flowering system, which is composed of lateral flowers only (or cymes, see below), is a characteristic feature of this type of inflorescence and is now referred to by the special term *florescence*. The term "florescence" should not be confused with the term "*inflorescence*," which has no specified morphological signification and may be used to designate any flower-bearing ramification system. (The same applies to the term "partial *inflorescence*," which can designate without any morphological relevance any part of a flowering system, while the term "partial florescence" means a distinct part of a florescence, namely a cymose branch.) Instead of ending in a single flower, as in the monotelic inflorescence, the floral axis here terminates in a multiflowered so-called polytelic florescence.

If the lateral flowers composing the florescences are provided with prophylls (Fig. 2 I), these may produce secondary flowers or dichasial or monochasial flowering systems from their axils (Fig. 2 II). This mode of ramification, in which the production of branches is restricted to the axils of prophylls of consecutive order, is called cymose (see Schimper, 1835; Wydler, 1851a: 305 ff.; Eichler, 1875: 34 ff., but not in the strict sense; Troll, 1957: 234 ff.; 1964: 63). The diverse sympodial ramification systems resulting from this mode of branching (Fig. 2 III–VI) are often briefly called cymes (cymae, see p. 231). In such cases the florescence consists of cymose *partial florescences* (pf) as, for example, in the inflorescences of most Scrophulariaceae and Labiatae (Fig. 3 III). Within both families, the derivation given here is verified by many transitional forms.

Below the florescence terminating the main axis there may be some branches that repeat the structure of the main stem by producing



FIGURE 1. Diagrams of a (I) monotelic and (II) polytelic inflorescence. *T*, terminal flower; *pc*, paracladium; *pc'*, *pc''*, paracladia of second and third order; *mf*, main florescence ("Hauptfloreszenz"); *cof*, co-florescence; *bi*, basal internode ("Grundinternodium"); *fi*, final internode ("Endinternodium"); *pz*, paracladial zone ("Bereicherungszone"); *inh.z.* inhibition zone ("Hemmungszone"). From Troll (in Troll & Weber, 1955), slightly modified.

florescences themselves and that therefore are also called *paracladia*. Their florescences are termed *co-florescences* in order to distinguish them from the main florescence of the main axis. The apices of the co-florescences remain *indefinite* like those of the main florescence. Thus the whole flower-bearing ramification system appears as a system of florescences: a (polytelic) *synflorescence*. In the case of a monotelic inflorescence, the synflorescence consists of a terminal flower and (monotelic) paracladia.

Within the polytelic synflorescences, the same zonation can be observed as in monotelic flowering systems (Fig. 3 II, III): an *enrichment zone* (Bereicherungszone: Troll), which precedes the main florescence, an *inhibition zone* (Hemmungszone: Troll), and in peren-

nials, an *innovation zone*. The three zones together form the so-called *hypotagma*. The florescence is separated from the paracladial zone by a *basal internode* (Grundinternodium: Troll), which may be of remarkable length.

It also proved to be useful to designate the ultimate internode preceding the terminal flower of a monotelic system by a special term: *final internode* (Grundinternodium, Fig. 1 I).

The polytelic type probably has been derived repeatedly from the monotelic during the evolution of angiosperms by reduction of the terminal flower and specialization of the paracladia of the monotelic system into either single lateral flowers or lateral cymes, which then constitute elements of the florescences, whereas the others are differentiated as par-

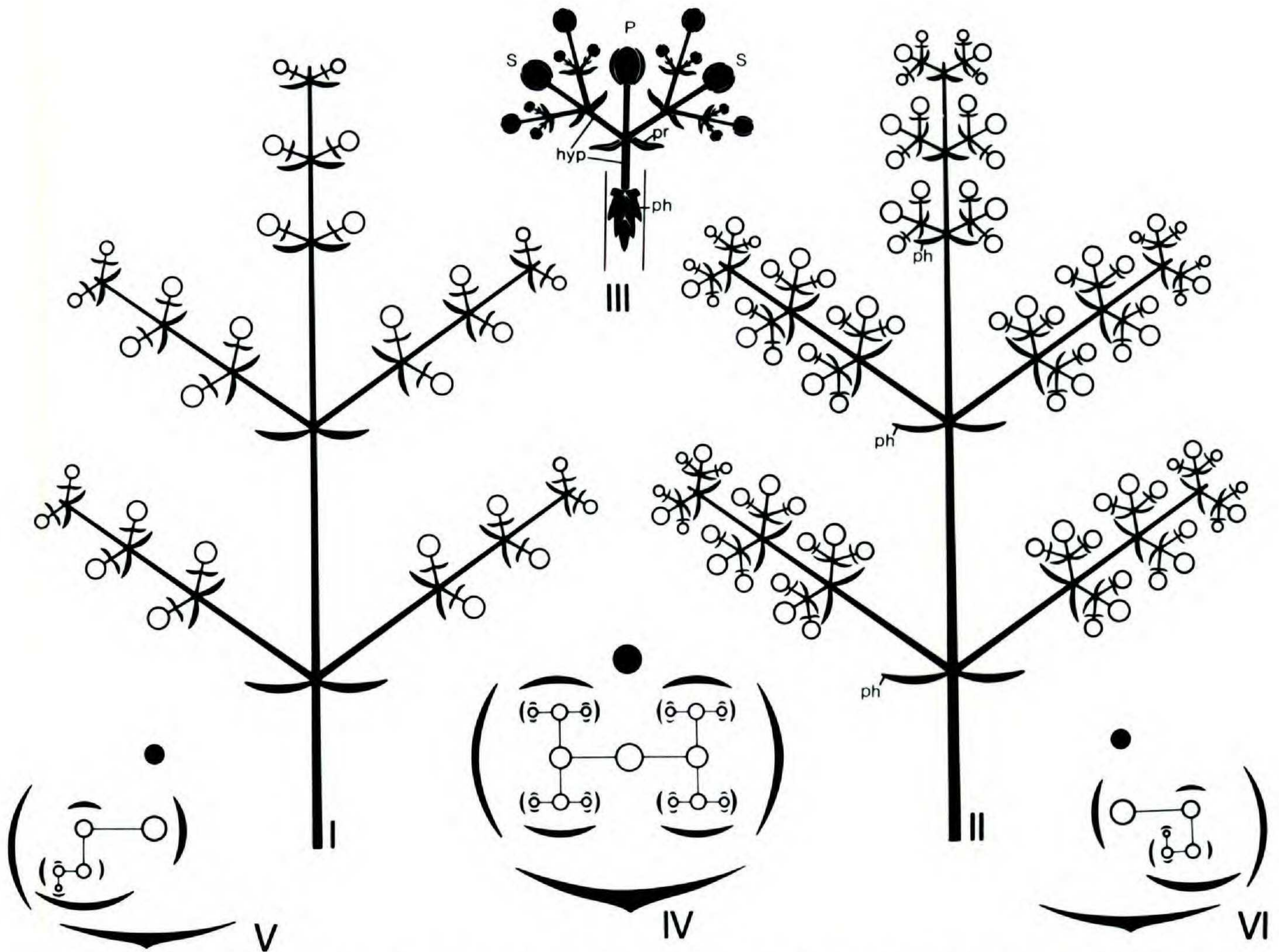


FIGURE 2. I, II. Vertical diagrams of polytelic inflorescences.—I. Heterothetic diplobotrys.—II. Diplothyrs; this inflorescence can be deduced from the diplobotrys in I by the assumption that the prophylls of second order are fertile. III–VI. Vertical (III) and transverse (IV) diagrams illustrating diverse forms of cymose ramification.—III, IV. Dichasium.—V, VI. Monochasia.—V. Scorpioid cyme (*cincinnus*).—VI. Helicoid cyme (*bostryx*). P, primary flower; S, secondary flower; ph, prophyll (“Tragblatt,” “Deckblatt”); pr, prophyll; hyp, hypopodium. III–VI from Troll (1959b), modified.

acladia (of the polytelic type), which themselves form florescences (Weberling, 1961, 1965, 1983a, b; Troll & Weberling, 1966).

In both monotelic and polytelic types, the different elements may vary in many different quantitative respects according to the principle of variable proportions: in polytelic synfloreences, the main florescence may be extended and the number of its flowers may be increased in many ways, or it may be reduced or even be missing altogether (truncate polytelic synfloreences). In both cases the paracladia may be well developed or reduced, their number may be increased, or they may be missing or modified in different ways. The development of paracladia may be basitonic or acrotonic (see below). Variation also exists in the diversity of phyllotaxis and

foliation, shortening or lengthening of the internodes in different parts of the plant, different intensity and different modes of ramification, and so on. Especially in woody plants the zonation of flowering systems can be altered extremely by, for example, the complete reduction of the inhibition zone.

An essential difference between the types seems to be that in inflorescences of the polytelic type the shoot apex of the inflorescence axis remains indeterminate. This also occurs, however, in some monotelic inflorescences in which the terminal flower aborts. In such *truncate monotelic synfloreences*, however, the paracladia usually end in terminal flowers, thus demonstrating the monotelic character of the whole system.

In many lianas, the growth of the main

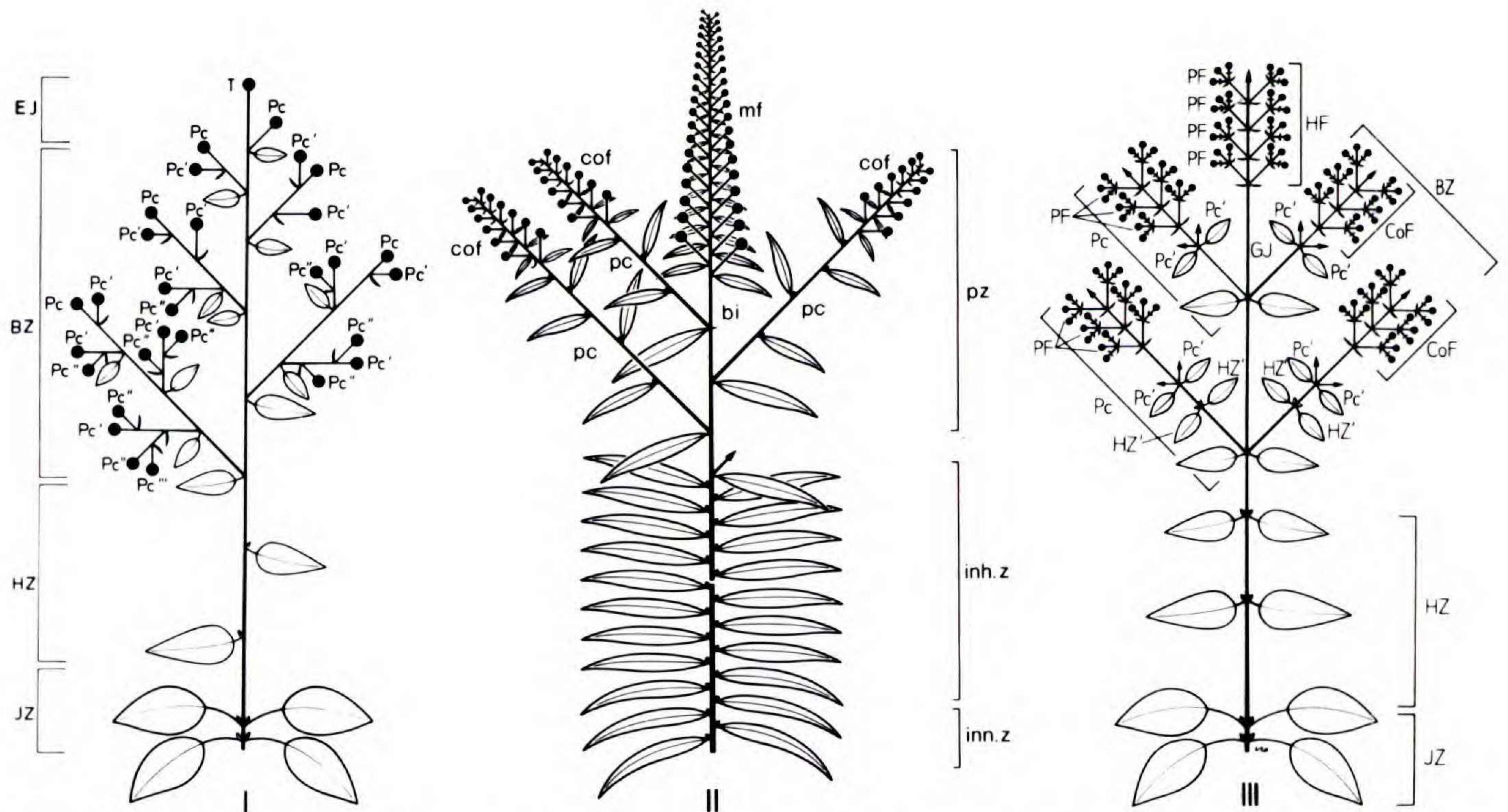


FIGURE 3. I. Diagram of a monotelic inflorescence in form of a panicle. *T*, terminal flower; *Pc*, *Pc'*, *Pc''*, *Pc'''*, paracladia of first to fourth order; *EJ*, final internode ("Endinternodium"); *BZ*, *pz*, paracladial zone (enrichment zone); *HZ*, *inh.z.*, inhibition zone; *JZ*, *inn.z.*, innovation zone.—II, III. Diagrams of polytelic inflorescences with the main florescence (*HF*, *mf*) and the co-florescences (*cof*) in form of botrya (II) or of thyrses (III). *GJ*, *bi*, basal internode; *pc*, *pc'*, paracladium of first and second order; *HZ'*, inhibition zone of *pc*; *PF*, partial florescence; the rest as in I.

axis is indefinite. Therefore the main axis, though it may produce lateral flower-bearing branches, never ends in a terminal flower. The sample applies to rosette geophytes with indefinite main axes, as in *Plantago* or *Phyllactis* (Valerianaceae). In the latter, the apex of the rosette changes periodically from the formation of absolutely sterile zones to the formation of fertile regions, in which thyrsoid "partial inflorescences" originate from the axils of the rosette leaves. (The same applies to the so-called *proliferating inflorescences* of many Myrtaceae.) In cases like these, the monotelic or polytelic character of the inflorescence is revealed by the monotelic or polytelic character of the paracladia.

Thus the question of whether the terms monotelic and polytelic correspond to the old classification of inflorescences into two groups called "indeterminate" (indefinite, racemose) and "determinate" (definite, cymose) must be answered in the negative. Apart from this answer, the statement given by Rickett (1955: 419), that "current usage" of this classification, "at least in English, is both confused

and inaccurate," still refers to this classification in general. To a great extent this is due to the fact that the "cymose type" is often equated with an "overtopping" of the (somewhat sympodial) branching system (Rickett, 1955: 426; Goebel, 1931: 81 ff.).

However, it is neither necessary nor possible to renounce all the classical descriptive terms used for the description and distinction of flower-bearing ramification systems. Many of these terms can be used without any change, and some need to be clarified and specified in their application. This also has been done by Troll (1964: 33 f.), who partly referred to Eichler (1875: 34 f.) in his classification of descriptive terms, which may be repeated here:

- I. *Simple inflorescences*: botrys (raceme), spike (stachys), spadix, umbella, capitulum.
- II. *Complex (compound) inflorescences*
 - a. with racemose partial inflorescences: diplobotrys (and related forms: bispica, bi-umbella, etc.), panicula.

- b. with cymose partial inflorescences:
thyrses (including thyrsoid), cymoid.

Among the compound inflorescences the panicle is distinguished by the main axis ending in a terminal flower (as do all of the branches). Thus the panicle is a determinate inflorescence, and this term never refers to any indeterminate inflorescence, as it often is used by English language authors.

If all branches of the panicle are reduced to single flowers (uniflorous paracladia), a botryoid system results that, however, still ends in a terminal flower and therefore is termed a "botryoid"; if the flowers are sessile, a spicoid. Complete reduction of all lateral flowers (all paracladia) leads to a uniflorous system (single terminal flower).

The term thyrses, which was often confused with the term panicle (Čelakovský, 1893: 45), needs some further comments too. (There is, of course, some connection between panicles and thyrsoids, as seen, e.g., in the so-called thyrso-paniculate systems of *Sambucus* and *Viburnum*: Troll & Weberling, 1966.) The term, used by Linnaeus for a "coarctate panicle of ovate form" (Rickett, 1955: 443), was specified by De Candolle (1827: 417) as "compound of small cymes along an axis of indefinite growth" (Rickett, 1955: 443; Bravais & Bravais, 1837: 197: "groupe de cimes disposées d'après l'évolution centripète comme les fleurs le sont dans l'épi"). It was applied, however, to determinate thyrso branching systems as well (see Troll, 1964: 63 f.).

Briggs & Johnson (1979: 177, 247) restricted the term thyrses to a "blastotelic inflorescence with a multinodate main axis that bears lateral cymes"; thus a determinate thyrso-like ramification system should be termed a thyrsoid (which appears consequent, as this term is comparable with terms such as botryoid, spicoid, cymoid in the terminology of Troll). Although we fear that a change of terminology used hitherto in so many publications might cause new confusion, we hesitantly follow this suggestion of Briggs & Johnson. Consequently, and in accordance with these authors, the adjective "thyrsoid"

must be replaced by "thyrsoidal" (thyrsoartig), while the adjective thyrsoic (thyrsoisch) should be used now for a thyrses in the restricted sense.

The terms used here are illustrated by Figure 2 II–VI. The vertical diagram in Figure 2 II shows a diplo-thyrsoic inflorescence. The distal part of it, comprising three pairs of lateral cymes, forms a simple thyrses (monothyrso, haplothyrso), whereas the branches originating from the two proximal nodes are thyrsoes themselves (named "Spezialthyrsoen" by Troll, "special thyrsoes," infrathyrso). In this diagram, the lateral cymes are triadic, i.e., comprising three flowers only. They may, however, produce more flowers by continuous branching from the consecutive axes (Fig. 2 III). The characteristic trait of this mode of ramification is that each axis before ending in a terminal flower produces two and only two leaves: the *prophylls*, which are mostly transversal-opposite and identical with the prophylls (the first two leaves) of other branches. In monocotyledons there is frequently only one prophyll, often in adaxial position. The internode preceding the prophyllar node is the *hypopodium*, the internode following the prophyllar node and terminating in the flower is the *epipodium*. If the two prophylls are separated by another internode, this is called the *mesopodium*. From the axils of the prophylls of the primary flower arise branches that end in the secondary flowers and bear two prophylls of second order. From the axils of the prophylls of second order the ramification can continue in the same way. This mode of cymose ramification can result in a complete symmetrical dichasium as shown in Figure 2 IV. In many cases, however, the continuation of the ramification is limited at a certain stage to one of the two prophyllar axils, thus resulting in the formation of a monochasium, either a scorpioid cyme (cincinnus, Fig. 2 V) or a helicoid cyme (bostryx, Fig. 2 VI). In the monocotyledons a rhipidium or a drepanium can be formed.

In thyrsoidal inflorescences, as displayed in a great variety of forms within the Caryophyllaceae for example, a high degree of

diversity can result from differences between paracladia in vigor of development. In many cases the paracladia are more extensively developed toward the base of the plant (*basi-tonic* ramification) or, if the paracladial zone is preceded by an inhibition zone, toward the middle of the plant (*basi-mesotonic*; in *mesotonic* ramification, vigor of the paracladia increases from both ends to the middle part of the flowering system), whereas in others the distal paracladia are the most vigorous (*acrotonic* ramification). Examples for these models can be found within the genus *Silene*.

In thyrsoids with decussate foliation and ramification (as in *Silene*), extreme acrotonic branching results in the exclusive development of the uppermost pair of cymose paracladia, which far overtop the main axis by vigorous development and copious branching. Such dichasia as represented, e.g., by *Silene vulgaris* (Moench) Garcke often have been regarded as ideal "cymose inflorescences." They are, however, connected by many transitional forms with basi-mesotonic thyrsoids as represented, e.g., by *Silene nutans* L. In other plants transitions can even appear in the same individual, if the subdistal pair of paracladia develops at a later stage. Thus these "dichasial" inflorescences do not represent an inflorescence type of their own but must be regarded as thyrsoids with acrotonic ramification. The complete inflorescence only simulates a cymose ramification, which actually takes place in the cymose paracladia. This induced Troll (1959a: 115; 1964: 102) to name this extreme form of an acrotonic thyrsoid a cymoid. In similar fashion, monochasial or pleiochasial overtopping of the main axis can be included in this term.

As is well known, foliation and phyllotaxis often change in the transition from the vegetative to the flower-bearing parts of a plant. The foliage leaves may be diminished from leaflike *frondose* to smaller *frondulose* organs or even convert by change of diverse proportions into *bracteose* organs (*bracts*), which are often more or less scalelike. The subtending leaves of the flower-bearing branches, the *pherophylls* (Briggs & Johnson, 1979:

179, 246; "Tragblatt," "Deckblatt"), may thus be frondose, frondulose, or bracteose.

The *mode of efflorescence* can, but need not be characteristic for the diverse forms of inflorescences. One should expect that anthesis of flowers follows the way of their initiation, advancing from, for example, the oldest flowers at the base of a botryoid to the top of this flowering system. In monotelic synflorescences, however, the terminal flower usually blooms before the neighboring laterals. To some extent this dominant position results from the fact that the organs of the terminal flower arise from the inflorescence apex immediately, whereas the lateral flowers are formed by lateral apices. Thus the terminal flower is somewhat in advance in relation to the ultimate lateral flowers. It is not rare for the flowers or partial inflorescences in the axils of the ultimate leaves preceding the terminal flower to be retarded or even to abort. Thus the terminal flower can be preceded by sterile leaves that are called "Zwischenblätter" (Nordhagen, 1937: 12; Troll, 1964: 15) or *metaxyphylls* (Briggs & Johnson, 1979: 179, 244). Beyond that, cases of a complete basipetal efflorescence—advancing from the top to the base of a flowering system—are not rare (*Meconopsis*). In the florescences of polytelic inflorescences, the efflorescence usually advances from base to apex (acropetal). For thyrses this means, of course, that an acropetal sequence of primary flowers that open first is followed and overlapped by a secondary sequence of the secondary flowers of the cymose partial florescences (Troll, 1957: 380 f.). There are also florescences with divergent efflorescence, the best known example may be *Dipsacus*. However, the sequence of paracladia in polytelic systems mostly unfolds in a basipetal order. Starting with the paracladia immediately below the main florescence, the progression of unfolding usually depends on the vigor of the individual and the length of the flowering period, thus determining the extension of the paracladial zone and the inhibition zone (Troll, 1950). Nevertheless, in annual or hapaxanthic plants this progression can reach the

base of the plant, and the most basal paracladia can, if they are fully developed, be the most vigorous.

ONAGRACEAE

Polytelic structure of inflorescences is manifested throughout the Onagraceae. The florescences are botrya or spikes. Even when the pedicels remain undeveloped, the inflorescences frequently (e.g., *Oenothera biennis* L., Fig. 4) look like botrya, because pedicels are simulated by the long gynoeceum of the epigynous flowers. In some taxa, e.g., *Epilobium alsinoides* Cunn. subsp. *tenuipes* (Hook. f.) Raven & Engelhorn, the pedicels lengthen after anthesis. Plants in the flowering state, as shown for the case of *Epilobium angustifolium* (Fig. 3 II), usually show a clear zonation: below the main florescences there is a more or less extended enrichment zone (paracladial zone, pz) which stretches down the primary axis until the development of paracladia is inhibited. Transition between this "inhibition zone" (inh.z., Hemmungszone) and the paracladial zone may be more or less abrupt. In perennials the axillary buds at the base of the whole stem do not develop within the same season but will give rise to innovation shoots at the beginning of the following season ("innovation zone," inn.z., Innovationszone).

Diversity in appearance of the different genera and species depends highly on quantitative variations of these zones, different lengths of the internodia, and different foliation of the florescences.

The phyllotaxis can be alternate or decussate, sometimes even verticillate mostly with three leaves at the same node. It is not rare to find that in the transition from the hypotagma to the main florescence the position of the leaves changes from decussate to alternate (e.g., *Epilobium montanum* L.).

The subtending leaves of the flowers can be quite different within the same genus. They can be bracteose as in *Fuchsia arborescens* Sims (Fig. 15 II) or foliaceous as in *Fuchsia magellanica* Lam. (Fig. 14), giving the inflorescence a "naked" or "leafy" shape. In many species of *Epilobium* or, for example,

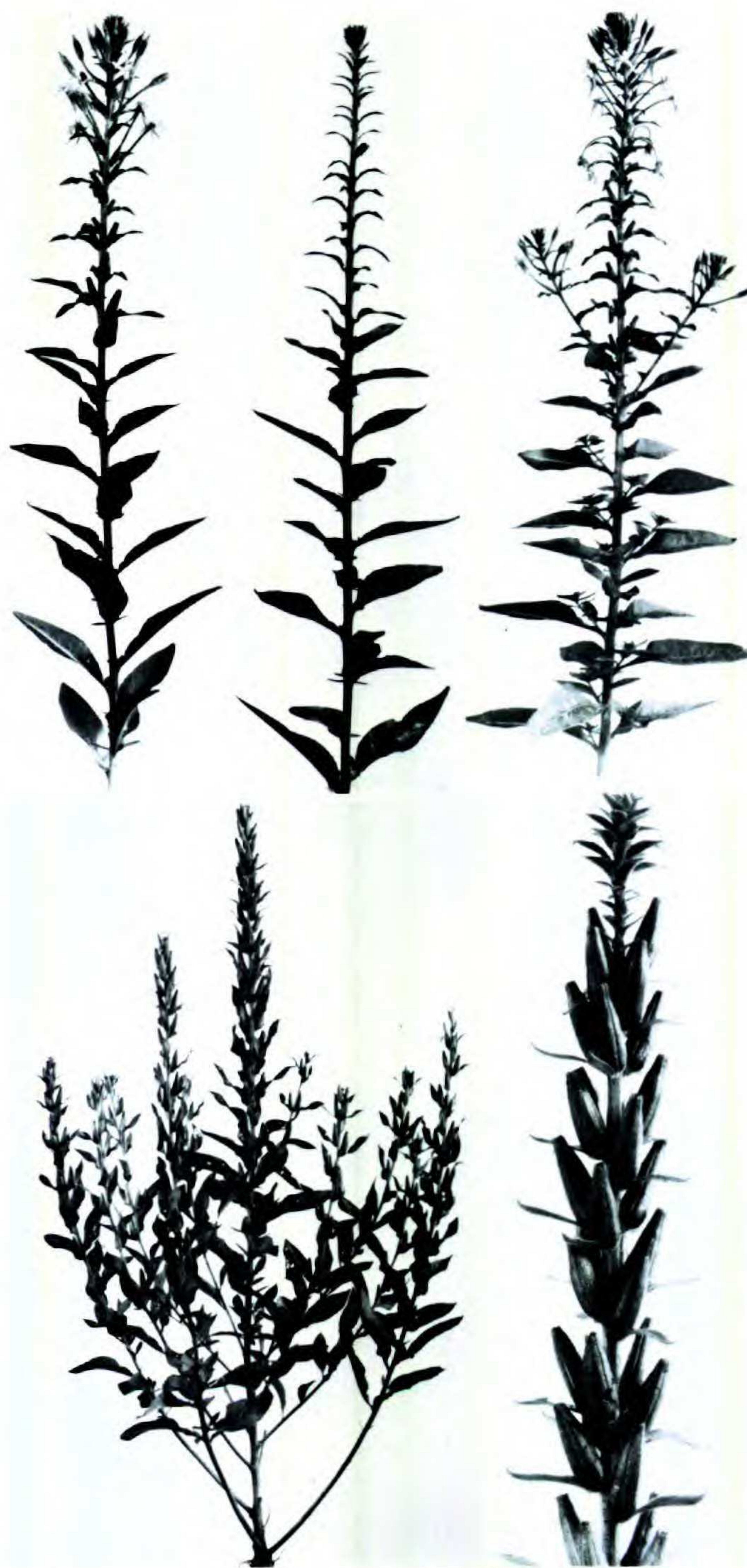


FIGURE 4. *Onagraceae*. *Oenothera biennis*.—Top, left. Flowering plant.—Top, center. The same plant with the flowers cut off to show the frondo-bracteose foliation.—Top, right. With developing paracladia.—Bottom, left. Plant with fully developed paracladia zone.—Bottom, right. Proliferation apex of the main florescence. (Original photographs from Troll.)

in *Oenothera biennis* (Fig. 4), they are leafy in the basal part of the florescences, diminishing distally, and finally becoming bracteose (frondo-bracteose foliation). Only in *Circaea* are the subtending leaves of the flowers missing. With the exception of the genus *Ludwigia*, the flowers do not bear prophylls.

Many representatives of the family are half-rosette plants, which means that the primary



FIGURE 5. *Onagraceae*.—I. *Oenothera rosea*.—II. *O. stricta*.—III. *O. fruticosa*.

axis starts with the formation of a leafy rosette and continues its development with elongated internodes. In *Oenothera biennis*, *O. muricata* L., and some other species, the rosette leaves that develop during the first year of the biennial life cycle do not persist until the plant is flowering. This plant in full development shows a large main florescence, a preceding paracladial zone, and a long zone of inhibition. This basi-mesotonic support of ramification is shown for *O. biennis* in Figure 4. In vigorous plants of *O. biennis* the paracladia can develop strongly and in great number (Fig. 4). In species forming typical half-rosette plants, such as *O. indecora* Cambess., *O. rosea* L'Hér., and *O. stricta* Ledeb., the development of vigorous "rosette shoots" (Rosettentriebe) can be observed (Fig. 5). They form a second series of paracladia separated from the upper paracladia by the zone of inhibition.

Usually the extension and the stoutness of the p.z. depends on the vigor and age of the plants. In the annual *Camissonia scapioidea* (Torrey & A. Gray) Raven and *C. walkeri*



FIGURE 6. *Onagraceae*. *Oenothera laciniata*, showing a small main florescence, a short inhibition zone, and vigorous rosette shoots. (USA. Texas: Brazos Co., N. Bean 331 (M, as *O. sinuata*).)

(A. Nelson) Raven subsp. *tortilis* (Jepson) Raven, the paracladial zone can be extended over the whole elongated part of the main shoot, leaving no residuum of the zone of inhibition between the upper paracladia and the rosette shoots ("simple or branching from the base . . . the stems quite simple above," Abrams, 1951: 206). These plants show a pronounced basitonic support in the development of the paracladia and a scapelike prolonged internode that precedes the main florescence. Especially within the *Oenothera* alliance (in tribe Onagreae), the proportions of the main florescence, the paracladial zone, and the inhibition zone and the development of the internodes can be modified in different ways and can be very characteristic for some taxa. Sometimes, in *Camissonia cheiranthifolia* (Hornem. ex Sprengel) Raven, for example, the development of paracladia can be restricted to the basal rosette. The reason is often that this rosette comprises the whole hypotagma while the main florescence is the only part of the axis with elongated internodes. The early development of these basal paracladia is shown for *O. fruticosa* L. in Figure 5.

In some species, for example, *Oenothera laciniata* (L.) Hill (Fig. 6), *Camissonia hirtella* (Greene) Raven, and *Calylophus hartwegii* (Benth.) Raven, even the main florescence often or always remains relatively short

and few flowered. In *O. caespitosa* Nutt., *Camissonia palmeri* (S. Watson) Raven, and many other species, the internodes of the primary axis, including the main florescence, are undeveloped throughout ("Caespitose perennial, acaulescent or nearly so," Abrams, 1951: 195). Among these species, *O. triloba* Nutt. (*O. rhizocarpa* Sprengel, *Lavauxia triloba* Spach), a hapaxanthic taprooted plant, is of special interest because of its basicarpous hygrochastic capsular fruits (Sernander, 1927: 73 ff.). In such cases the paracladia, however, can be well developed, forming plagiotropic (Figs. 7, 8) or ascendent branches with frondose (co-)florescences.

In other rosette plants, for example, *Camissonia graciliflora* (Hook. & Arn.) Raven (Fig. 15 III), even the paracladia, if developed, remain short, the whole plant forming a single rosette (also *Oenothera ovata* Nutt., *O. xylocarpa* Cav., *O. nana* Griseb., Figure 9, *C. tanacetifolia* (Torrey & A. Gray) Raven, Figure 10, *C. subacaulis* (Pursh) Raven, and *O. formosa* Brandegee), or a caespitose tuft.

In contrast to *Oenothera triloba*, which always retains its rosette stage, *O. macrocarpa* Nutt. subsp. *macrocarpa* (*O. missouriensis* Sims) is a perennial tap-rooted geophyte. After the juvenile rosette stage, it grows with slightly prolonged internodes and can develop innovation shoots, which can innovate secondarily. The same could possibly apply to *O. californica* (S. Watson) S. Watson, which Abrams (1951: 195) described as "perennial from underground rootstalks, rather coarse stemmed, rarely simple."

In the fruiting plant of *Oenothera triloba* (Fig. 8), the top of the primary axis is crowned by a bunch of foliage leaves as a result of the proliferating growth of the florescence axis. This proliferation may occur repeatedly in the same primary axis, thus forming zones with buds of paracladia alternating with single flowers in the axils of more or less foliaceous leaves. Proliferation can be observed in many additional species of *Oenothera*, for instance, *O. macrocarpa* and *O. biennis* (Fig. 4), and in many other members of the family, since

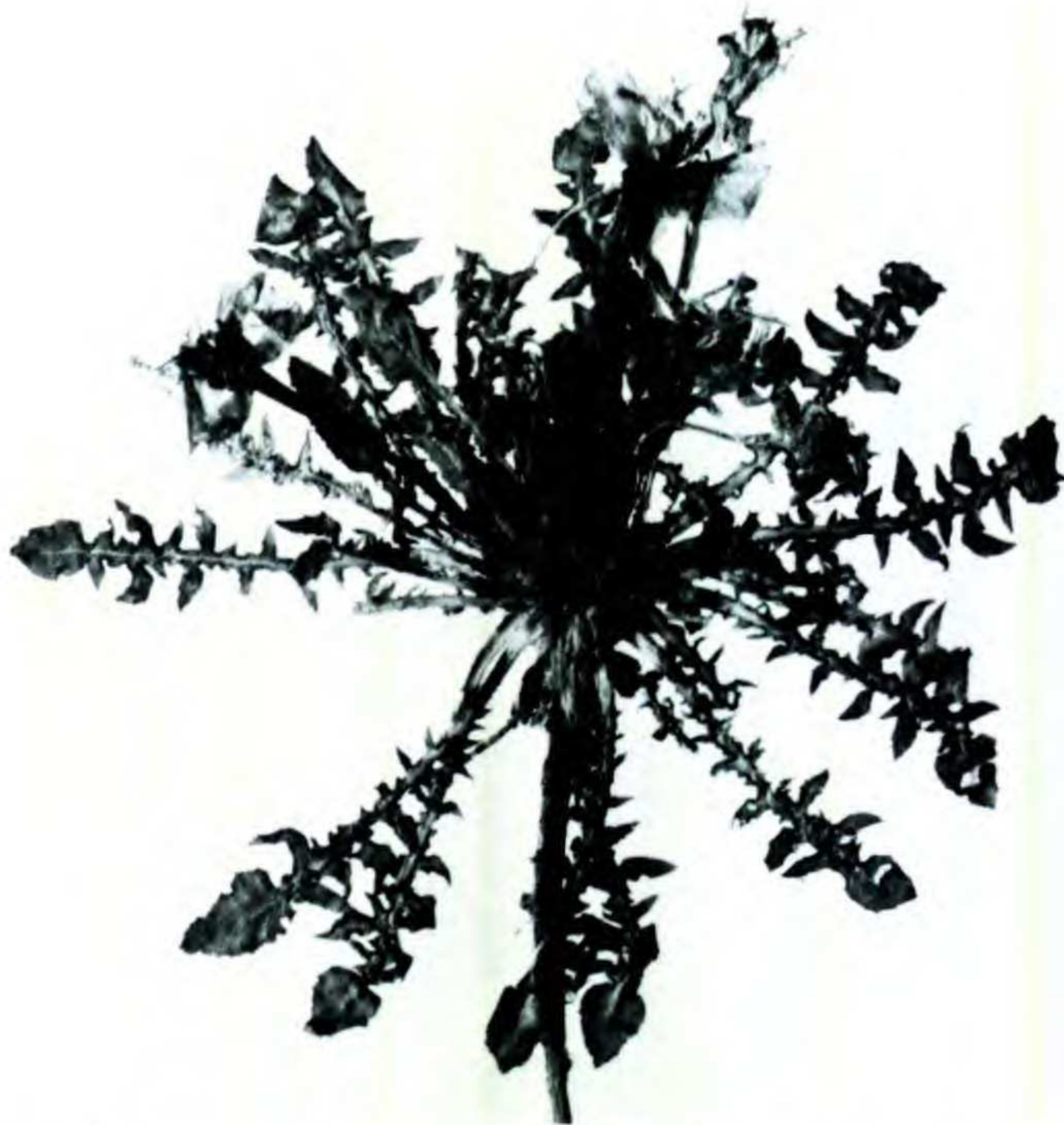


FIGURE 7. *Onagraceae*. *Oenothera triloba*. (USA. Texas: Tarrant Co., Fort Worth, A. Ruth 70 (M).)

the predisposition is frequently given by a strong florescence axis with more or less leafy pherophylls.

In *O. triloba*, *O. macrocarpa*, and *O. biennis*, it is the apex of the main florescence that returns to vegetative growth (Spätprolifikation, Troll, 1960: 116, proliferation of the florescence, retarded proliferation), whereas *O. multicaulis* Cav. (Figs. 11, 12) does not form a main florescence at all. Rather, it develops long paracladia from the axils of rosette leaves (Frühprolifikation), which can grow straight upright (Fig. 11) or more or less ascendent (Fig. 12).

In most herbaceous genera of *Onagraceae* the same architecture and zonation as described for the basi-mesotonic ramified *Epilobium angustifolium* (Fig. 3 II) and for *Oenothera biennis* (Fig. 4) can be observed. This applies to many species of *Epilobium* and all or most species of *Boisduvalia*, *Clarkia* (except species with decumbent or prostrate stems), *Gaura* and allied genera, *Lopezia*, and *Circaea*, although some species of *Boisduvalia*, e.g., *B. densiflora* (Lindley) S. Watson (Troll, posthumous notices), can be branched from the base.

Plagiotropic growth, often connected with proliferation, is also characteristic for *Clarkia*

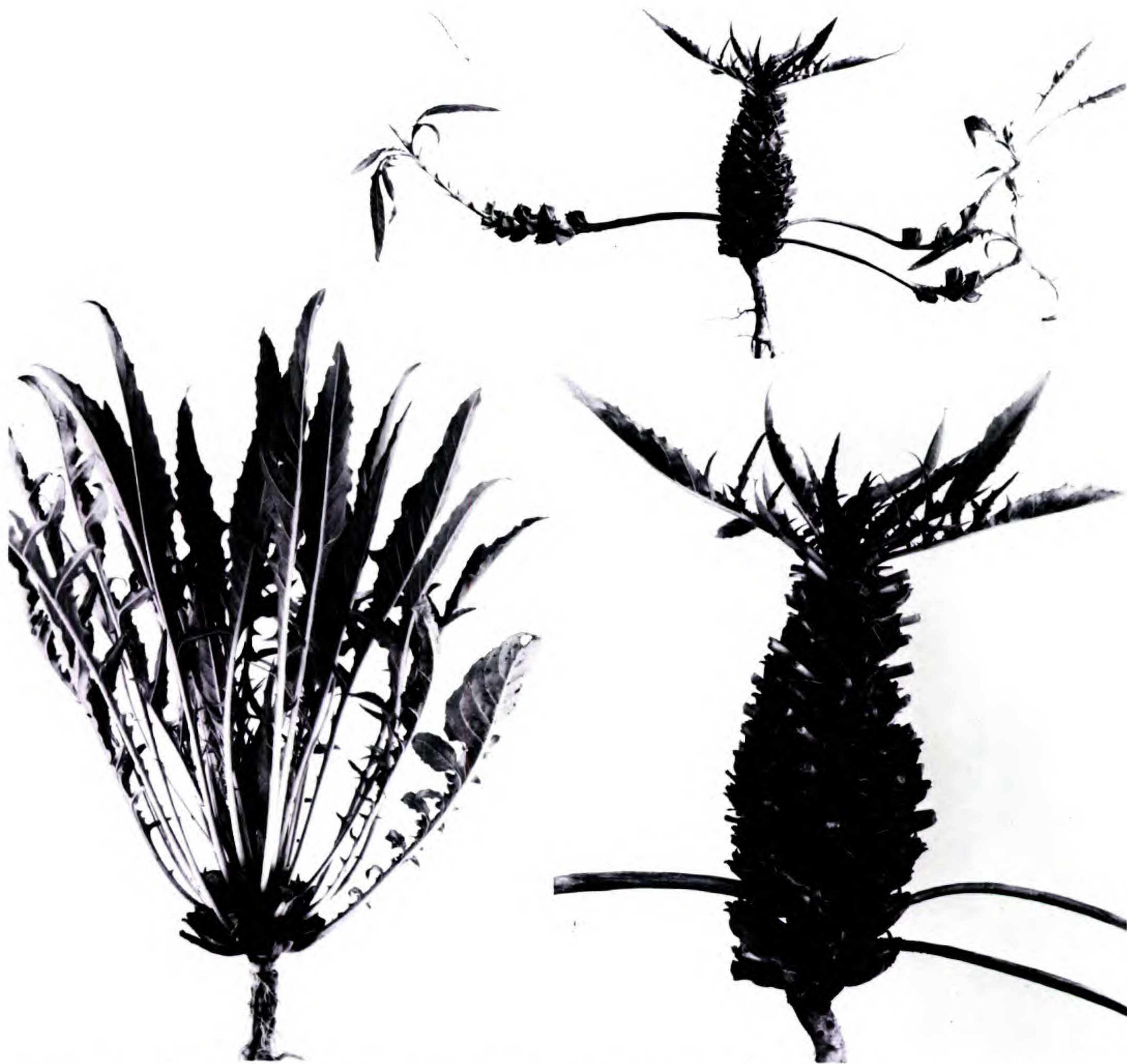


FIGURE 8. *Onagraceae*. *Oenothera triloba*.—Left. Fruiting plant with proliferating main axis.—Top, right. Fruiting plant with terminal vegetative rosette and stolonlike fruiting and proliferating paracladia.—Bottom, right. Detail. (Original photographs from Troll.)

prostrata Lewis & Lewis, *C. davyi* (Jeps.) Lewis & Lewis (Lewis & Lewis, 1955, fig. 11b, c), *Camissonia strigulosa* (Fischer & Meyer) Raven, and many species of *Ludwigia*.

Plants growing under severe environmental stresses may develop reduced inflorescences only. This is especially common in annuals. Often only the main florescence is formed, and in extreme but not uncommon cases only the lowermost flower of the main florescence comes to anthesis. *Clarkia bottae* (Spach) Lewis & Lewis (Fig. 13 I) is an example. In such cases this lowermost flower

can be erected in pseudoterminal position, which also is characteristic for *Epilobium alpinum* L. f. *pusillum* Hausskn. The same occurs facultatively in *E. montanum* (Fig. 13 II).

For the genus *Epilobium* two features must be mentioned, each of them characteristic for a great number of species. In many species the buds of the innovation zone develop more or less proleptically into epigeal or subterranean stolons. If these stolons creep at the surface of the soil, their leaves are more or less foliaceous, as in *E. alpinum* L. The subterranean stolons bear scalelike cataphylls.

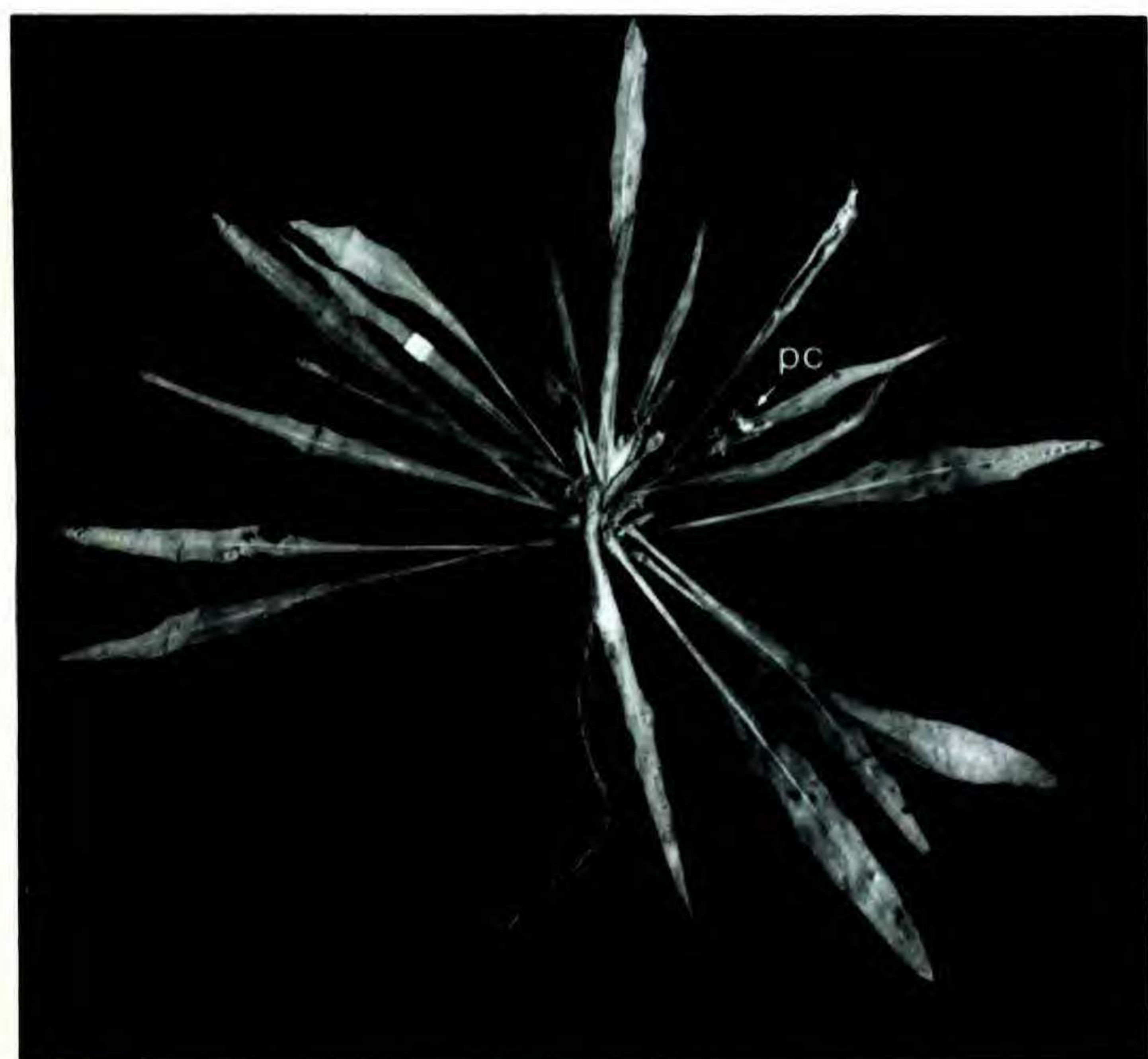


FIGURE 9. *Onagraceae*. *Oenothera nana*. All internodes of the primary axis, including the main inflorescence, remain short; this also applies to the paracladia (pc). (Peru. Puno: above Chimu, K. A. Santarius 2056/364 (M).)



FIGURE 10. *Onagraceae*. *Camissonia tanacetifolia*. (USA. Washington: Spokane Co., July 1884, Suksdorf s.n. (M).)



FIGURE 11. *Onagraceae*. *Oenothera multicaulis*. Plant with rosette-leaved proliferating main shoot and flowering paracladia. (Peru: between Huancayo and Jarpa, Müller 2345/75 (M).)

Their internodes may be very slender (*E. lineare* Muhlenb., *E. obscurum* Schreber) and often form small bulbs at their ends, especially well developed in *E. palustre* L. (Irmisch, 1847; Warming, 1918: 348; Troll, 1937: 811, fig. 639). In others the stolons are somewhat thickened, forming storage organs in this way (*E. hirsutum* L., Fig. 14). There are also many transitional forms between subterranean and epigeal stolons, which then develop foliaceous leaves in place of scales (*E. hirsutum*), and between stolon-forming innovation buds and those that remain short (the latter in *E. montanum*, *E. collinum* Gmelin, *E. roseum* Schreber, transitional in *E. parviflorum* Schreber, and *E. lanceolatum* Seb. & Mauri). In *E. palustre* there occur also transitional ascendent shoots with foliaceous leaves coming to flower in the same year as the main shoot and thus forming proleptical-



FIGURE 12. *Onagraceae*. *Oenothera multicaulis*. Plant with proliferating main shoot with rosetted leaves and ascendent paracladia with co-florescences. (Peru: Huancayo. Santarius 2204/717 (M).)



FIGURE 14. *Onagraceae*.—Left. *Epilobium hirsutum*; plant with vigorous subterranean stolons.—Right. *Fuchsia magellanica*; inflorescence. (Original photographs from Troll.)

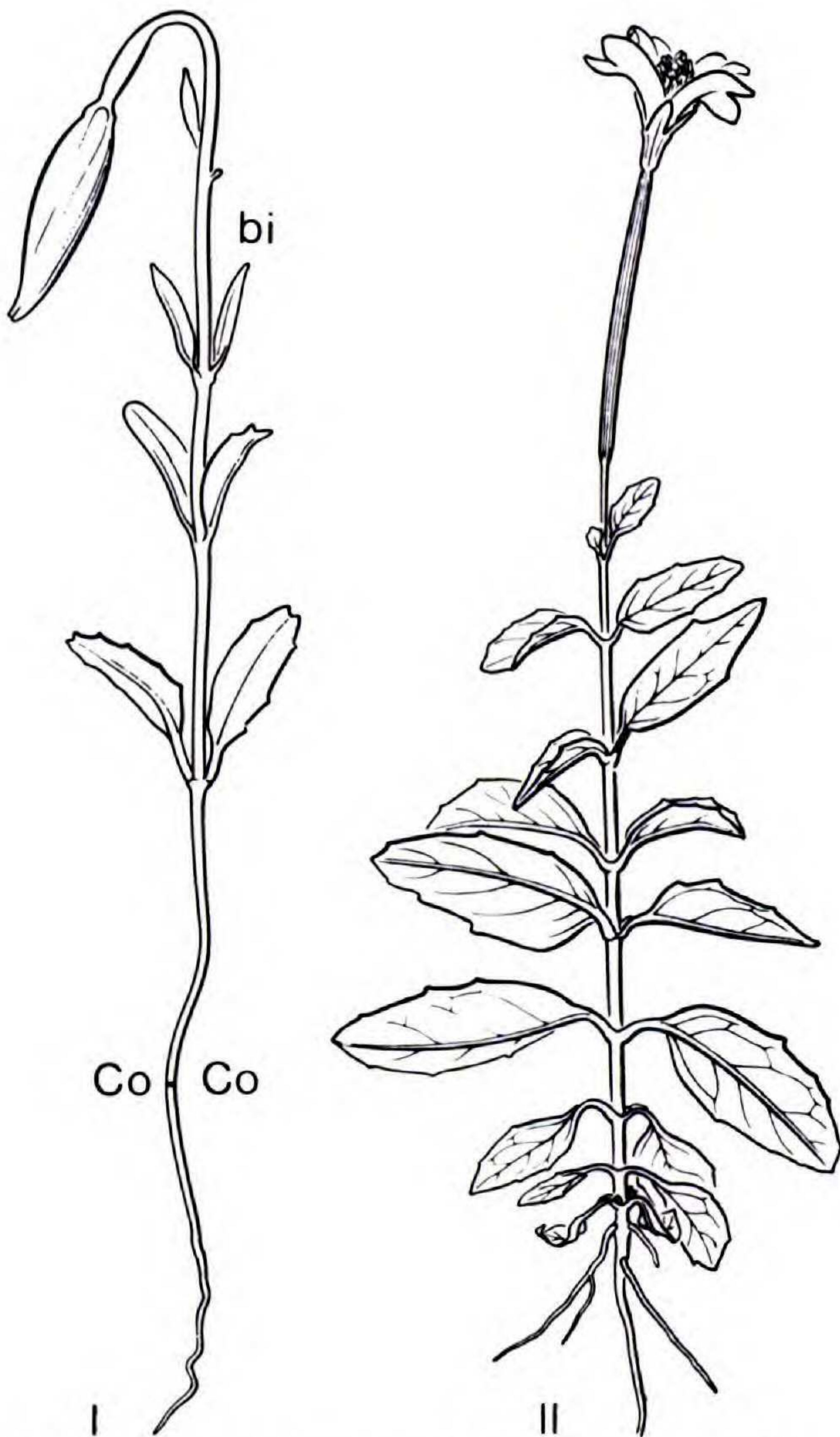


FIGURE 13. *Onagraceae*. One-flowered dwarf forms of *Clarkia bottae* (I) and *Epilobium montanum* L. (II). *bi*, basal internode; *Co*, scars of the cotyledons. (Original drawings from Troll.)

antheal (see Müller-Doblies & Weberling, 1984) innovation shoots, while normally it takes until the next season for the stolonlike or short remaining innovation shoots to develop into a new flowering system. (For discussion of different modes of perennation in *Epilobium*, see Keating et al., 1982.)

A second peculiarity is especially characteristic for a number of species belonging to the series *Similes*, *Microphyllae*, and *Sparsiflorae* Hausskn., distributed in Australia, Tasmania, and New Zealand. These species show a more or less plagiotropic growth correlated with proliferation of the florescence apex, which seems to be a constant feature within the three series. "All of the leaves are opposite" (Raven & Raven, 1976: 15), and "the stem creeps and roots at the nodes, and continues growing vegetatively beyond the area where the flowers are produced." Thus the apex of the florescence regularly returns to a vegetative phase in which paracladia are developed and returns again to the production of a certain number of flowers. In *Epilobium nummulariifolium* R. Cunn., a node bearing a pair of flowers may be followed by two nodes with paracladia, but more frequently one of the axils of a pair of leaves produces a flower,

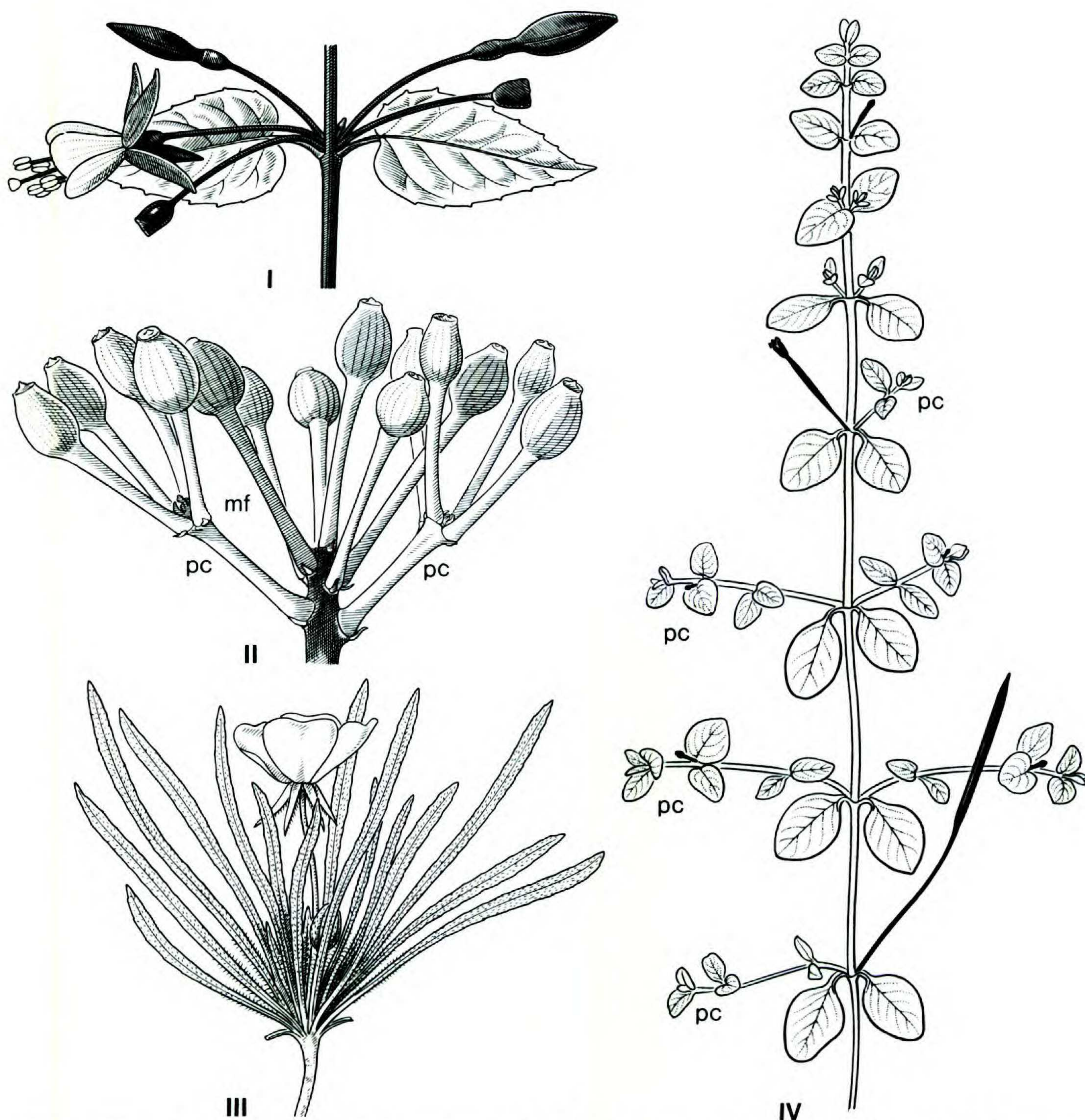


FIGURE 15. *Onagraceae*.—I. *Fuchsia coccinea*; node of the florescence with regular and accessory flowers.—II. *F. arborescens*; inflorescence with main florescence (mf) and paracladia (pc).—III. *Camissonia graciliflora*; habit (after J. W. Hook.).—IV. *Epilobium nummulariifolium*. (I, II, IV original drawings from Troll.)

while the other one bears a paracladium (Fig. 15 IV). Troll (unpubl. notes) found the primary axis passing over to plagiotropic growth after the unfolding of the cotyledons. The axils of the cotyledons produced paracladia. According to Raven & Raven (1976: 15) this "habit has evolved independently on at least seven occasions among the Australasian species, as indicated by the morphological, genetic, and geographical relationships of the species involved: 1) *E. willisii*; 2) *E. mac-*

ropus; 3) *E. pedunculare*; 4) *E. crassum*; 5) *E. margaretiae*; 6) *E. brunnescens*, *E. pernitens*, *E. nerteroides*, and *E. nummulariifolium*; and 7) *E. komarovianum* and *E. angustum*. There is presumably an ecological solution as to why this peculiar plant form, unknown elsewhere in the world, should have evolved repeatedly in Australasia."

Within the genus *Ludwigia* (including *Jussiaea*) one can find species that show the typical zonation as described for polytelic



FIGURE 16. *Onagraceae*.—*Left*. *Ludwigia suffruticosa*.—*Center*. *L. alata*.—*Right*. *L. octovalvis* (*L. capitata*). (Original photographs from Troll.)

plants with botrytic florescences. *Ludwigia suffruticosa* (L.) Gomez serves as an example (Fig. 16). The main inflorescence is a frondose botrys. The same applies to the paracladia, which are preceded by an inhibition zone. Axoscopic accessory buds can be observed accompanying the paracladia as well as the single flowers of the florescences. The apex of the inflorescence axis proliferates repeatedly: after having produced single lateral flowers forming the main florescence, it develops a paracladial zone and then returns to produce single flowers again. This zonation found in *L. octovalvis* is also found in *L. alata* Ell. (Fig. 16) and *L. perennis* L. In the latter the pherophylls within the florescences are somewhat smaller than in the preceding paracladial zone. Here the paracladia mostly comprise a co-florescence only, since the prophylls bear flowers in their axils already. The axoscopic accessory buds within the florescence form small flower-bearing branches, while those that accompany the paracladia remain undeveloped.

In *Ludwigia virgata* Michaux, development of the paracladia usually is suppressed. The plants are extremely heterophyllous, bearing lanceolate leaves in the proximal part of the hypotagma and linear leaves in the distal part, whereas the foliation of the main florescence consists of small bractlike leaves. *Ludwigia octovalvis* (Jacq.) Raven resembles

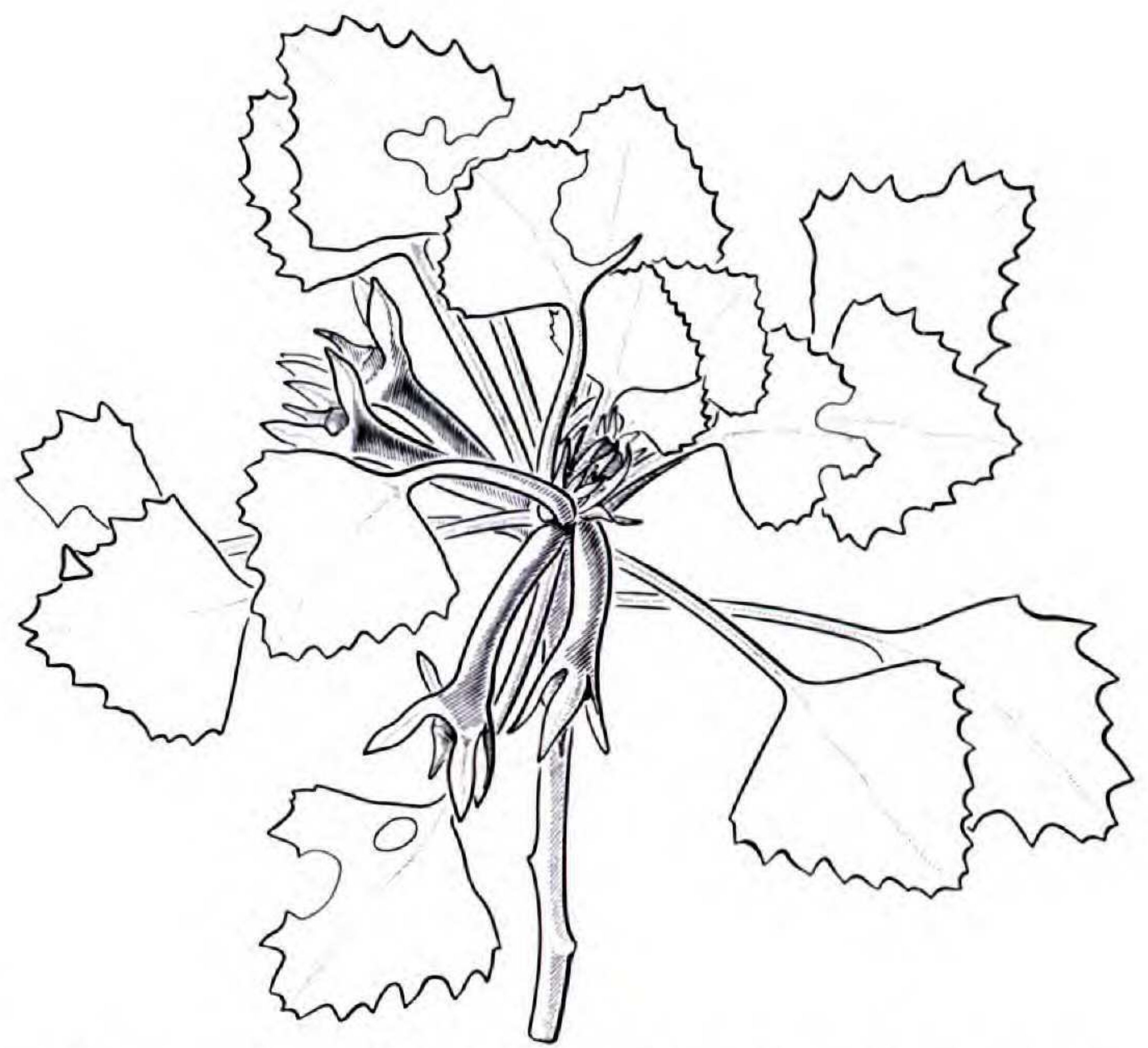


FIGURE 17. *Trapaceae*. *Trapa natans*; flowering rosette. (Deutsch-Mühlenweiher, Saarbrücken, 1904, Ruppert s.n. (M).)

L. virgata in the suppression of the paracladia, but the flowers of the main florescence of *L. octovalvis* (= *L. capitata* Michaux) usually are condensed into a head by suppression of internode development (Fig. 16). At the base of the plants, Troll (unpubl. notes) sometimes observed stolonlike innovation shoots.

On the other hand, we could not find a main florescence in herbarium specimens of *Ludwigia abyssinica* A. Rich. The specimens investigated only had paracladia ending in a botrytic florescence, their foliation being bracteose in the upper paracladia and frondobracteose in the lower paracladia. If this preliminary result proves to be true, *L. abyssinica* has a truncate polytelic synflorescence.

Ludwigia palustris Ell. differs from the preceding species by having plagiotropic growth. The plant, which grows in stagnant or slow-flowing water or on muddy soil, develops roots from the nodes and different forms of leaves depending on ecological conditions. In these features *L. palustris* resembles species such as *L. helminthorrhiza* (Martius) Hara (*Jussieua natans* Humb. & Bonpl.) and *L. adscendens* (L.) Hara (*J. repens* L.), which are well known for peculiar respiratory roots that develop at the nodes in addition to normal roots. They also show a more or less pronounced heterophylly. Here again the inflo-

rescence apex regularly proliferates and returns to flower formation. In *L. peduncularis* (Wright ex Griseb.) Gomez (*L. clavellina*) a pair of flowers often is followed by a pair of paracladia. In the picture of *L. helminthorrhiza* given by Humboldt & Bonpland (1805, t. 3, under *Jussieua natans*), each flower is accompanied by a vegetative accessory branch.

The most interesting species of *Ludwigia* is *L. sedoides* (Kunth) Hara, an aquatic herb in which the branches end in floating rosettes. The rosettes are formed by alternate leaves that gradually differ in the length of their petioles, thus forming a configuration similar to a rosette window.

Usually the flowers are described as solitary in the axils of the foliage leaves. Actually they all form a botrytic main florescence which proliferates, however, after the formation of only a few flowers, forming a vegetative flowerless zone and then returns to flower production. Thus the flower-bearing zones are interrupted by vegetative zones. Paracladia that repeat the architecture of the main shoot seem to develop rarely only from the more remote parts of the stem.

In all of these respects *Ludwigia sedoides* is completely congruent with *Trapa natans* L., Trapaceae (Fig. 17). The submerged leaves of *Trapa*, however, are pinnatifid and thus differ from the floating leaves that have a rhombic lamina and somewhat inflated petioles, which keep the rosette floating.

In the ligneous (*Fuchsia*, *Hauya*) or suffruticose Onagraceae, the architecture of the inflorescences does not differ fundamentally from that of the herbaceous genera.

In *Fuchsia* the diversity of inflorescences mainly depends on differences of foliation, development of the internodes, and degree of ramification within the flower-bearing parts. As was shown already, the difference between the bracteose and the leafy character of the prophylls (Figs. 14, 15 II) has a great effect on the appearance of the plants. In *F. magellanica* the leafy botrytic florescences proliferate frequently and often repeatedly, giving the impression that there are "flowers

solitary in the axils of leaves." From the vegetative zones of the "interrupted florescences" paracladia can develop. Accessorial flowers can occur in a phylloscopic sequence (Fig. 15 I). Quite a different impression is given by the botrytic florescences of *F. triphylla* L., *F. coccinea* Sol., and *F. fulgens* Mociño & Sessé (see Raimann, 1893b, fig. 94A), the foliation of which is bracteose or frondo-bracteose. In *F. boliviana* Carr. the pendant botrytic frondo-bracteose main florescence and co-florescences are hanging by the inclination of their prolonged basal internodes, while the flower-bearing zone is more or less condensed (Fig. 18). The bracteose inflorescence terminating the foliaceous shoots of *F. arborescens* Sims (Fig. 18) is often called a panicle but comprises a botrytic main florescence and a smaller or greater number of paracladia, which are restricted to their co-florescences. The inflorescences of *Hauya elegans* DC. subsp. *cornuta* (Hemsley) Breedlove & Raven is a leafy proliferating few-flowered spike. Although the structure of the inflorescences within the woody Onagraceae seems to be clear, the position of the flower-bearing branches within the whole ramification system should be examined in comparative investigations regarding the different growth forms of the ligneous plants.

LYTHRACEAE

The diverse forms of ramification found in the inflorescences of Lythraceae have been carefully investigated and described by Koehne (1883). Thus we only need to treat some new fundamental and comparative aspects here. The phyllotaxis is usually decussate, rarely alternate; sometimes verticils with three or many (e.g., species of *Rotala*) leaves are formed. With some exceptions (*Cuphea* sect. *Lythrocuphea* and some other species) prophylls are nearly always present within the inflorescences. Eichler (1878b: 478) named as the only exceptions *Cuphea* subgen. *Cuphea* (subgen. *Lythrocuphea* Koehne) and the secondary flowers within the cymes of *Lythrum* species.



FIGURE 18. *Onagraceae*. Inflorescences of *Fuchsia arborescens* (left) and *F. boliviana* (right). (Original photographs from Troll.)

Within the family only the genera *Galpinia*, *Lagerstroemia*, *Lawsonia*, *Rhyncho-calyx* (now treated as *Rhynchocalycaceae*), and *Woodfordia* are characterized by monotelic inflorescences.

The inflorescence of the ligneous *Lagerstroemia indica* L. (Figs. 19 I, 20 I) is a diplothyrsoid (a diplothyrsse with terminal flower) with three- to seven-flowered cymes. A remarkable feature of this inflorescence is that effloration takes place from base to top, though the terminal flower of the whole system precedes the neighboring lateral ones. The same applies to the terminal flowers of the thyrsoïd paracladia in the proximal part of the inflorescence. Correlated with this mode of effloration is the delay in the formation of the ultimate lateral flowers below the terminal flower, which can be more or less impeded (Fig. 20 Ia). In case of complete reduction of the uppermost paracladia their subtending bracts appear as metaxyphylls.

Generally *Lagerstroemia tomentosa* Presl shows the same mode of ramification as *L. indica*. In *L. calyculata* Kurz, *L. hypoleuca* Kurz, and *L. speciosa* Pers., however, the distal part of the inflorescence bears a considerable number of uniflorous paracladia forming a botryoidlike zone. This also occurs in the thyrsoïd paracladia at the base of the inflorescence, which apparently are more numerous and vigorously developed in these species. In any case, a careful comparative examination of the inflorescences of the numerous species of this genus is needed in order to find out if the peculiarities mentioned here are useful for diagnostic and systematic aims.

The mode of effloration found in *Lagerstroemia indica* can also be observed in *Lawsonia inermis* L. (Fig. 19 II), which differs from *L. indica* in that the ramification of the cymes does not exceed the three-flowered stage (Fig. 20 II). On the other hand, the number of flowers of the inflorescence fre-



FIGURE 19. *Lythraceae*.—I. *Lagerstroemia indica*.—II. *Lawsonia inermis*; flowering branches. (After Koehne, 1893.)

quently is increased by accessory phylloscopic branches of first (as_1) and second (as_2) order. They can form a single flower provided with two prophylls, as in pc_2 to pc_4 , or can develop into triads (pc_5) and even into thyrsoids (pc_6). The highest degree of ramification and most vigorous development of accessory branches takes place at the base of the whole inflorescence. The formation of accessory branches

can be repeated within the paracladia (pc_5 , pc_6) and even within the accessory branches themselves (as_1 in pc_6). The diagrams in Figure 20 III–V give additional information about the serial position of the accessory branches. Accessory branches or flowers are very common within the whole family.

Lagerstroemia parviflora Presl (Fig. 21 I) has advanced to the differentiation of a

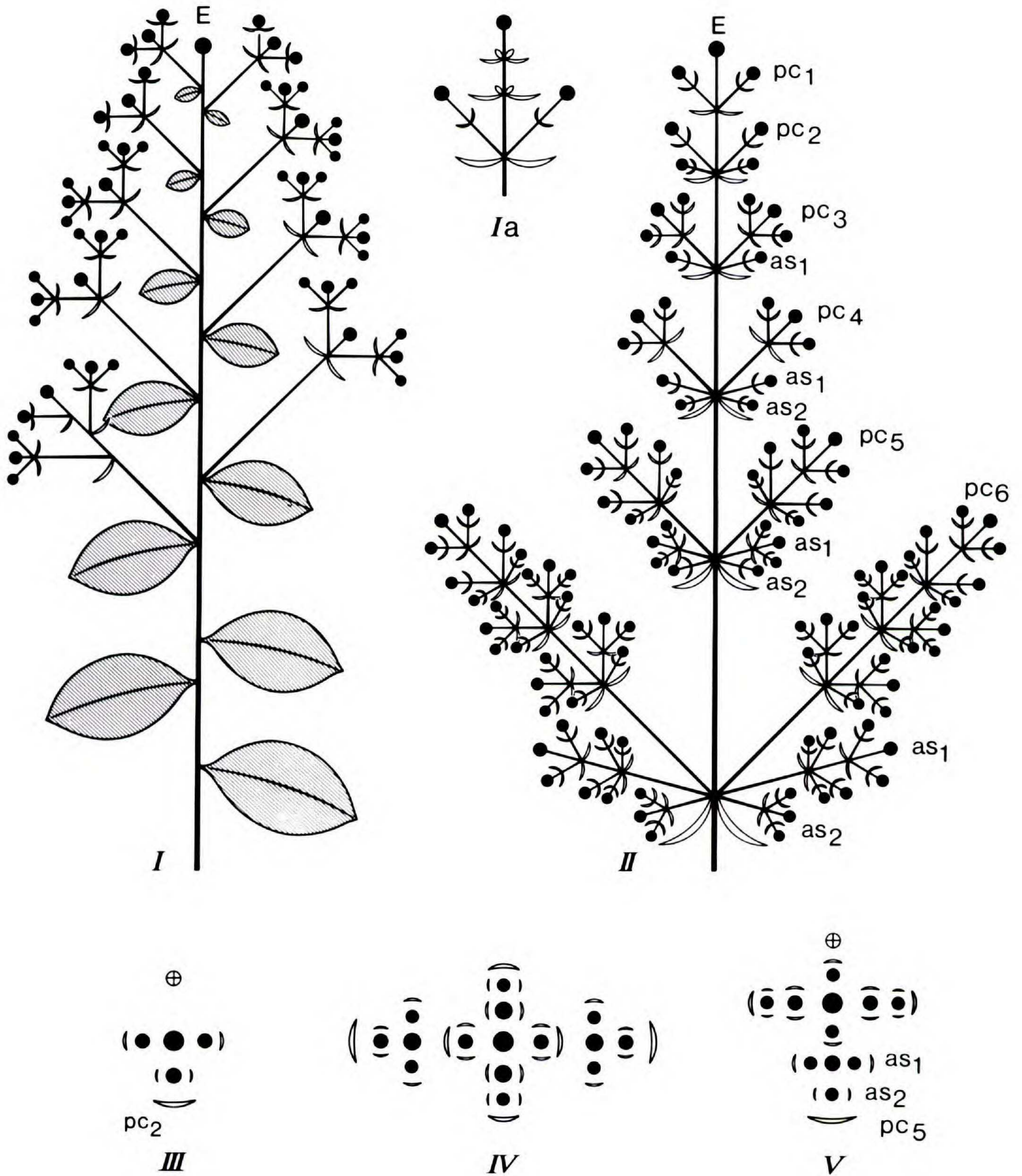


FIGURE 20. *Lythraceae*. *Lagerstroemia indica* (I, Ia) and *Lawsonia inermis* (II-V). Vertical projections of flowering branches (I, II) and horizontal projections of pc_2 (III), pc_5 (V) with accessory branches as_1 and as_2 , the distal part (pc_1 - pc_2) of the inflorescence in II (IV). Ia is terminal flower of another inflorescence of *Lagerstroemia indica* with two preceding pairs of bracts with undeveloped axillary buds. (From posthumous notices of W. Troll, except Ia.)

long shoot-short shoot system in which flower formation is restricted to the short shoots (brachyblasts), while the long shoots (macroblasts) continue the vegetative growth. In this case the buds of the short shoots are protected by a series of bud scales and kept undeveloped

until the next vegetation period. At the moment of their unfolding and flowering the long shoot has lost its leaves already. The flowering short shoot proliferates. Thus the inflorescence consists of paracladia only, which form botryoids rising from the axils of normally

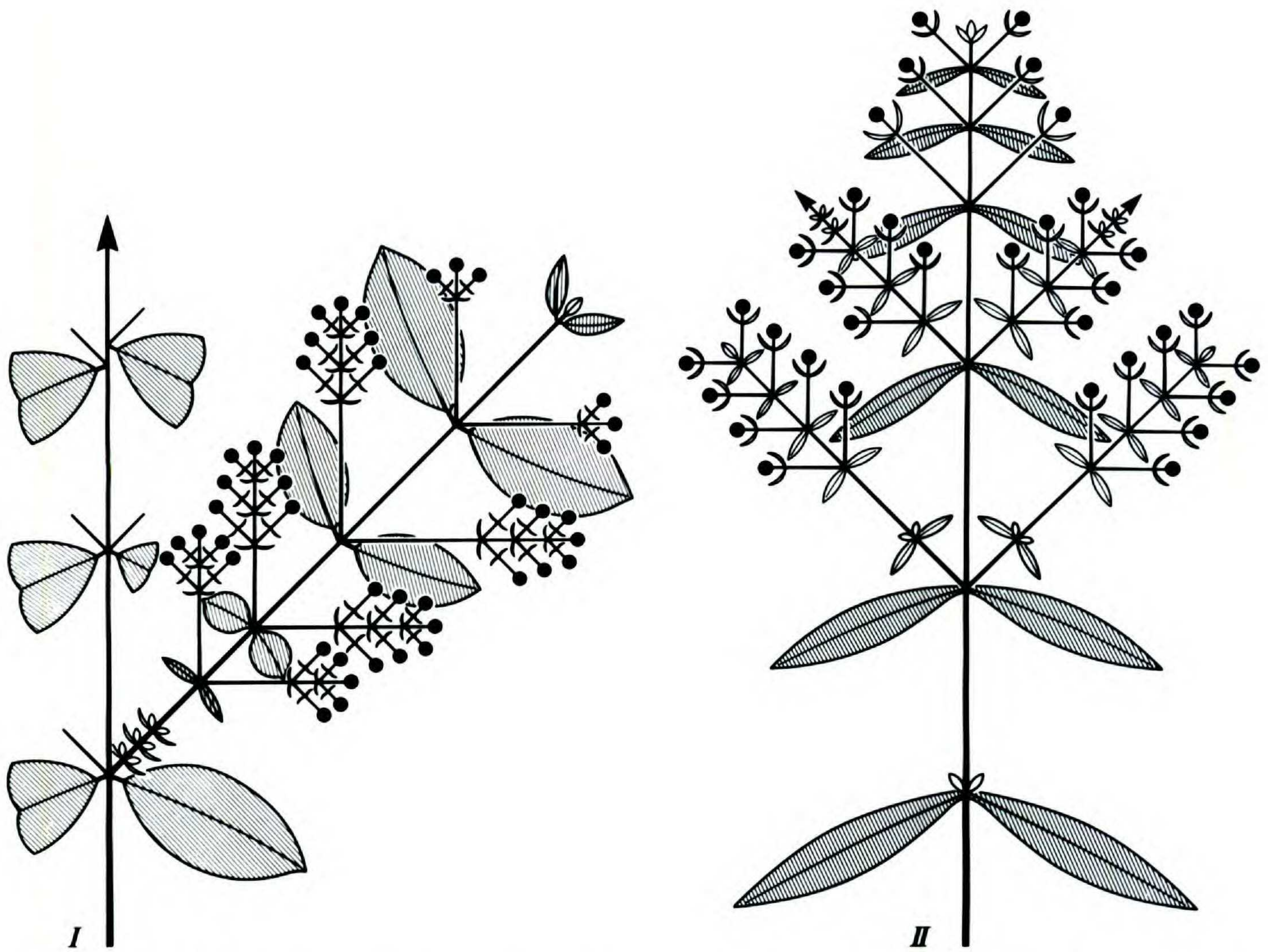


FIGURE 21. *Lythraceae*. Vertical projections of flowering branches.—I. *Lagerstroemia parviflora*; piece of a last year's vegetative long shoot with a flowering short shoot.—II. *Lafoensia replicata*. (From posthumous notices of W. Troll.)

developed or, at the base of the short shoots, very small foliaceous leaves. The basis of the brachyblast that bears bud scales may be interpreted as a zone of inhibition or perhaps also as an innovation zone.

If *Punica* (formerly *Punicaceae*) ought to be included in *Lythraceae*, forming subfamily *Punicoideae*, it could be placed close to *Lagerstroemia* for its monotelic inflorescences. These inflorescences, however, are highly reduced and frequently limited to their terminal flower. They may develop one or two decussate pairs of uniflorous paracladia originating from the axils of bracteose leaves. The uniflorous paracladia bear prophylls that are inserted immediately below the flower. Most of these lateral flowers degenerate sooner or later.

Sonneratia (formerly *Sonneratiaceae*), which is regarded now to form subfamily Son-

neratioideae within the *Lythraceae*, also has monotelic inflorescences: terminal botryoids with two or three decussate pairs of uniflorous paracladia that bear large prophylls immediately below the flowers. At least the lowermost paracladia arise from the axils of foliage leaves. Sometimes only the terminal flower develops (*S. acida* L. f.).

The genus *Duabanga*, which was formerly included in *Sonneratiaceae* and now is regarded to represent subfamily *Duabangoideae* of the *Lythraceae*, has terminal few-flowered panicles in which ramification only sometimes goes beyond the formation of Pc'.

Crypteroniaceae, formerly sometimes joined with *Sonneratiaceae*, differ fundamentally from *Sonneratia* by polytelic di- to pleiotelitic inflorescences of panicle-like appearance with frondo-bracteose (*Axinandra* Thwaites, *Dactylocladus* Oliv.) or mainly

bracteose (*Crypteronia* Bl.) foliation and many-flowered botrya. In the axils of the lowermost and foliaceous leaves of the flowering system we could observe well-developed botrytic accessory branches.

Sometimes we found the terminal flower of the inflorescence of *Lagerstroemia speciosa* missing, though terminal flowers still were present in all paracladia. One might overestimate this fact, however, if one interprets this occurrence of truncate monotelic inflorescences as first indication of a gradual transition to the polytelic type within the family. In any case polytelic inflorescences occur in most Lythraceae.

The inflorescence of *Galpinia transvaalica* N. E. Br. resembles those of *Lagerstroemia* in the terminating leafy branches and in its paniclelike structure: the inflorescence axis and all floriferous branches end in terminal flowers. Its foliation, however, is frondulose to bracteose.

In contrast to *Galpinia*, *Lawsonia*, and most species of *Lagerstroemia*, the flower-bearing systems of the shrubby genus *Woodfordia* (*W. floribunda* Salisb., *W. uniflora* (A. Rich.) Koehne) are brachyblastlike branches originating in the axils of foliaceous leaves that are still present during anthesis. They are thyrses or diplo-thyrses (in the narrow sense, cf. Fig. 2 II) with frondulose leaves on their main axes. Since they often bear a series of cataphylls at their bases, it seems likely that they do not unfold immediately after initiation but remain as buds for a while, perhaps to endure an unfavorable season. Frequently these brachyblasts are accompanied by phylloscopic accessory branches of similar shape.

In the flowering systems of *Lafoensia*, another ligneous genus comprising large trees or shrubs, all axes bearing more than one pair of leaves proved to be auxotelic or anauxotelic (see p. 290). The inflorescence of *L. replicata* Pohl, which may serve here as an example (Fig. 21 II), shows a complete reduction of cymose branching. Thus a terminal and several pairs of lateral botrylike structures with acropetal effloration are formed. They can be

interpreted as the terminal main florescence and the co-florescences of a polytelic system. The same applies to *L. acuminata* DC., *L. pacari* St. Hil., *L. puniceifolia* DC., and *L. densiflora* Pohl. The deciduous prophylls of the flowers are situated immediately at the base of the flowers. In other species, as in *L. nummulariifolia* St. Hil., the number of flowers is diminished.

While in the *Lafoensia* species treated here the subtending leaves within the inflorescences are more or less foliaceous, *Physocalymma scaberrimum* Pohl is characterized by bracteous foliation throughout the whole flower-bearing system that terminates vegetative branches. This system is a diplo- or pleiobotryum with a large paracladial zone (Fig. 22 I). The axes of all botrya end in a vegetative bud. According to Koehne (1893), flowering of this tree takes place when the plants have lost their leaves. In the shrubby *Pemphis madagascariensis* (Baker) Koehne, the production of flowers seems to be limited to brachyblastlike branches which, however, proliferate like the macroblastic main axis. The botrytic flower-bearing zones comprise a few flowers only (Fig. 22 II). *Pemphis acicula* Forster, the second species of the genus, is similar.

A gradually progressing differentiation of the ramification system into flower-bearing short shoots and vegetative long shoots can be seen within the genus *Ginoria* Jacq. As reported by Koehne (1883: 115) in *G. americana* Jacq., the flower-bearing branches arise from the axils of foliaceous leaves. After the appearance of a pair of bud scales, these twigs develop several pairs of foliaceous leaves that bear single flowers in their axils (Fig. 23 I). At a later stage the twigs pass over to vegetative growth. *Ginoria spinosa* and *G. glabra* Griseb. are reported to be similar, but the flowering branches are shorter with fewer flowers and do not proliferate regularly.

In *Ginoria curvispina* Koehne, the flower-bearing brachyblasts unfold in the season after their initiation, when their prophylls are already lost (Fig. 23 IIa). Their foliation begins with one to three pairs of cataphylls

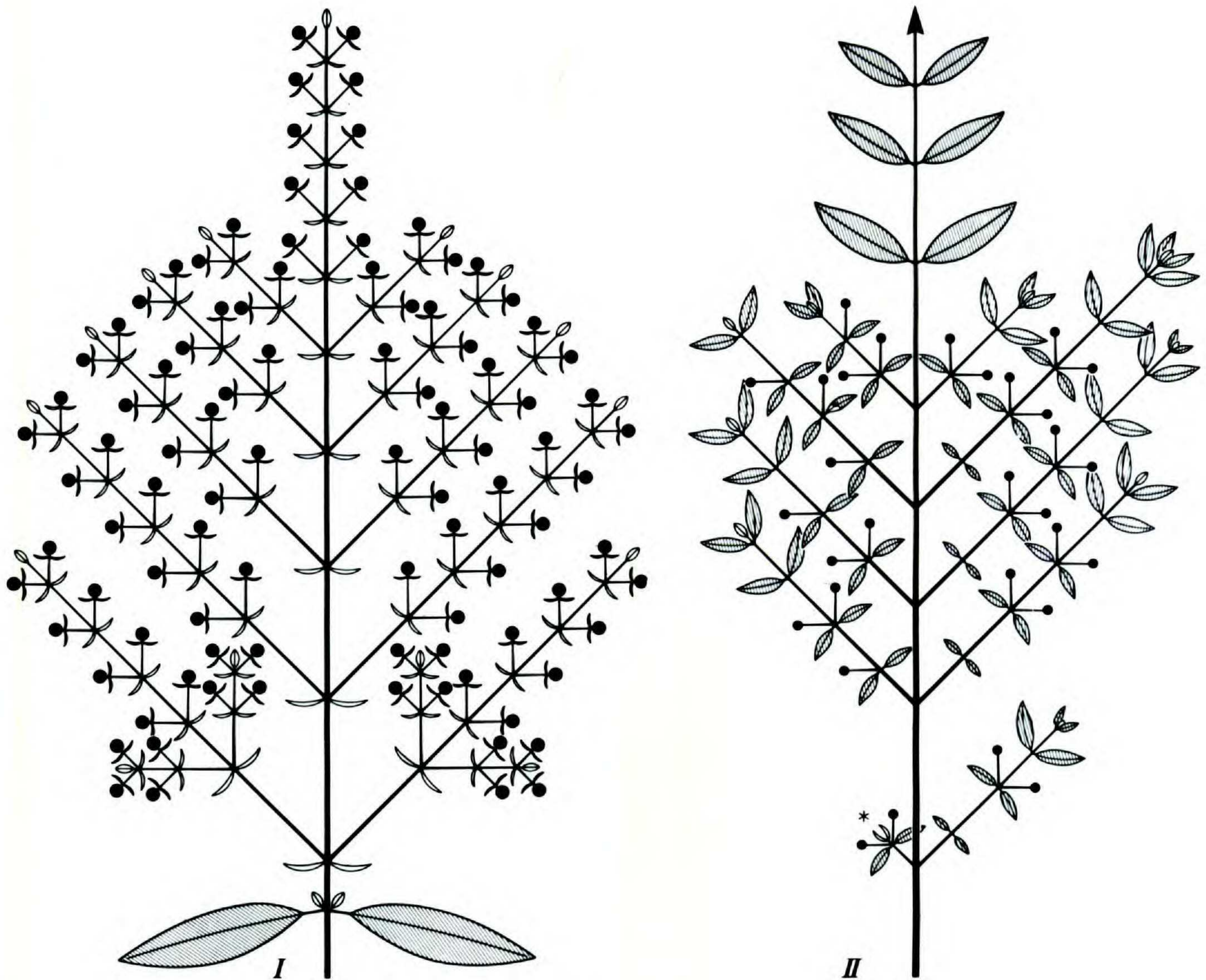


FIGURE 22. *Lythraceae*. Vertical projections of flowering branches.—I. *Physocalymma scaberrimum*.—II. *Pemphis madagascariensis*. (From posthumous works of W. Troll.)

followed by foliaceous leaves. The whole brachyblast can bear one to four pairs of single flowers that can originate in the axils of the cataphylls as well as in the axils of the foliaceous leaves. Finally the brachyblasts proliferate.

According to Koehne (1883: 116), the foliaceous leaves of the brachyblasts resemble those of the macroblasts but measure only one-fourth of their size.

Thus the brachyblasts with their botrytic main florescences contrast conspicuously with the vegetative macroblasts, which at their distal end can continue growth with the development of a new annual shoot. According to the observations of Koehne, these new shoots can also bear single flowers in the axils of their lowermost foliaceous leaves (Fig. 23 IIb). Koehne also reported that two similar long

shoots can originate at the very base of the annual shoot and also bear up to four pairs of flowers (Fig. 23 IIc). Thus the limitation of flower production to the short shoots seems not to be complete yet.

In *Ginoria diplusodon* Koehne (Fig. 23 III), the brachyblasts remain shorter, their foliation consists of scales, one to three pairs of which can bear flowers in their axils, thus forming a short botrys. (Sometimes the prophylls of these flowers bear secondary flowers.) Even here the annual shoots continuing the macroblasts (Fig. 23 V) develop one to three pairs of single flowers originating in the axils of cataphylls at the base of the annual shoots (Koehne, 1883). *Ginoria rohrii* (Vahl) Koehne is similar, but the brachyblasts are shorter and the two- to eight-flowered florescence is umbel-shaped (Figs. 23 IV, 24);

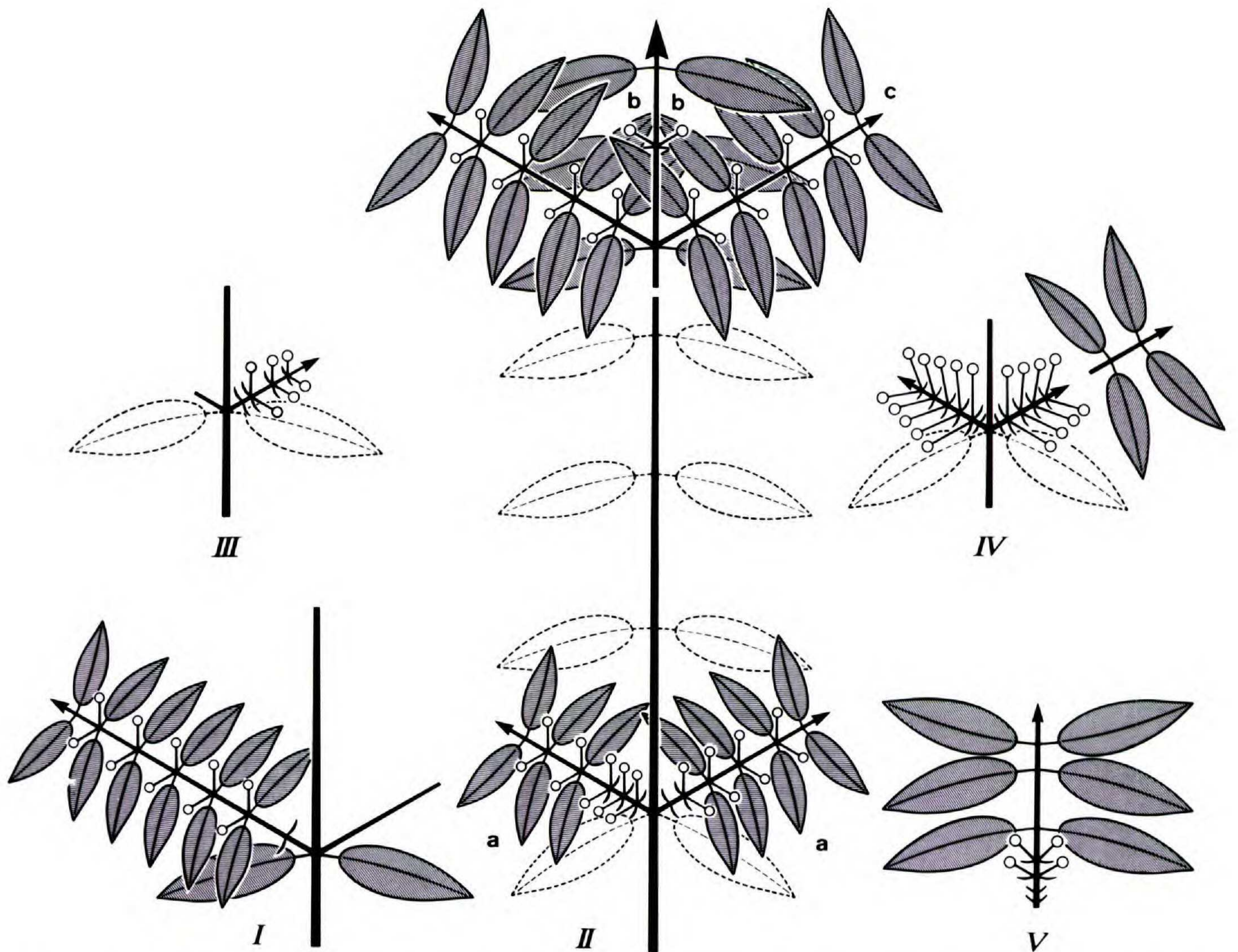


FIGURE 23. *Lythraceae*. Vertical diagrams of flowering shoots.—I. *Ginoria americana*; proliferating brachyblast.—II. *G. curvispina*; last year's macroblast with flowering and proliferating brachyblasts (a), single flowers in the axils of proximal foliaceous leaves of the new annual shoot (b), and lateral macroblasts (c) developing from the axils of proximal foliaceous leaves of the new annual shoot. These lateral macroblasts can also bear single flowers in the axils of their proximal foliaceous leaves.—III. *G. diphusodon*; bracteose flowering brachyblasts in the leaf axils of a last year's macroblast.—IV. *G. rohrii*; brachyblasts which later can proliferate.—V. *G. diphusodon*; base of an annual shoot (macroblast) with flowers in the axils of the uppermost (bud) scales. Prophylls of the flowers omitted. (Construction according to report by Koehne (1883) and to our results.)

the prophylls are sterile. The brachyblasts unfold when the macroblast is already defoliated. The uppermost brachyblasts are reported to proliferate occasionally. According to Troll (unpubl.), the terminal bud of the macroblast often fails. Then the macroblast is continued by the development of the uppermost lateral buds. Their foliation begins with two or three pairs of bud scales. The distal pair can be frondulose; according to Koehne (1883: 117), the flowers originating in the axils of the bud scales may bear a second flower in the axil of one of their prophylls.

Although the florescences of the ligneous *Lythraceae* such as *Ginoria*, *Lafoensia*, *Pem-*

phis, and *Physocalymma* present themselves as botrya or spikes, the basic form of the florescence in the polytelic *Lythraceae* is a thyse (in the narrow sense, i.e., without terminal flower). Among the ligneous taxa this is demonstrated by *Adenaria*: in *A. floribunda* Kunth, the flower-bearing twig is a foliaceous, proliferating thyse with many-flowered cymes, which by abbreviation of all internodes except the epipodia become umbel-shaped or headlike (Fig. 25). *Pehria* (= *Grislea*), as seen in *P. compacta* (Rusby) Sprague, is said to be similar in this respect (Koehne, 1893); the same applies to *Decodon verticillatus* (L.) Ell.

Within the suffruticose and herbaceous taxa

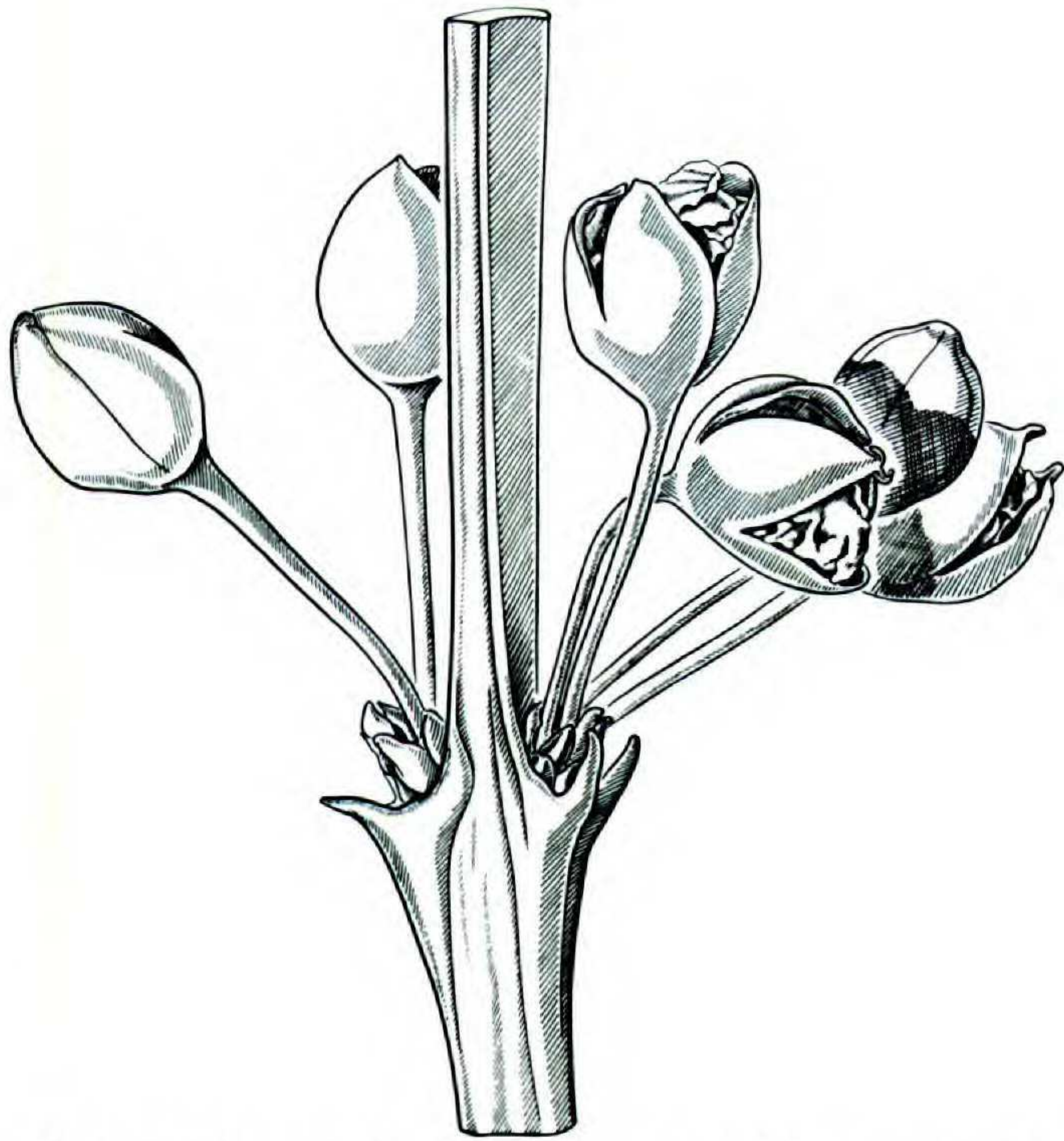


FIGURE 24. *Lythraceae*. *Ginoria rohrii*; macroblast with two brachyblasts. (June, 1907, Eichinger s.n. (M).)

there are also many groups with copiously branched thyrses. As an example, *Nesaea crassicaulis* (Guill. & Perr.) Koehne (Fig. 26 I) may be mentioned. Its partial florescences are loosely branched with only the hypopodia remaining relatively short, whereas in others, for example, *N. pedicellata* Hiern, even the hypopodia are prolonged and form long peduncles. In *N. aspera* (Guill. & Perr.) Koehne all internodes remain short, and the partial florescences form many-flowered glomerules (see also *N. sarcophylla* Koehne in Koehne, 1903: 227, fig. 43E).

Frequently the partial florescences are reduced to uniflory, thus converting the thyrses into a botrys or spike. This applies to some species of *Nesaea* (e.g., *N. linifolia* Hiern (Fig. 28 III) and *N. baumii* Koehne), most species of *Lythrum*, and all species of *Pleuraphora*, *Cuphea*, *Heimia*, *Peplis*, and *Diplusodon*. In *Rotala*, only one species, *R. serpiculoides* Hiern, is reported to have 3–12 flowered dichasia (Koehne, 1883: 124), while in *Ammannia* reduction of the cymes to uniflorous elements occurs facultatively in many species.

A remarkable arrangement of flowers within the botrytic florescences can be observed in *Rotala wallichii* Koehne. It was reported

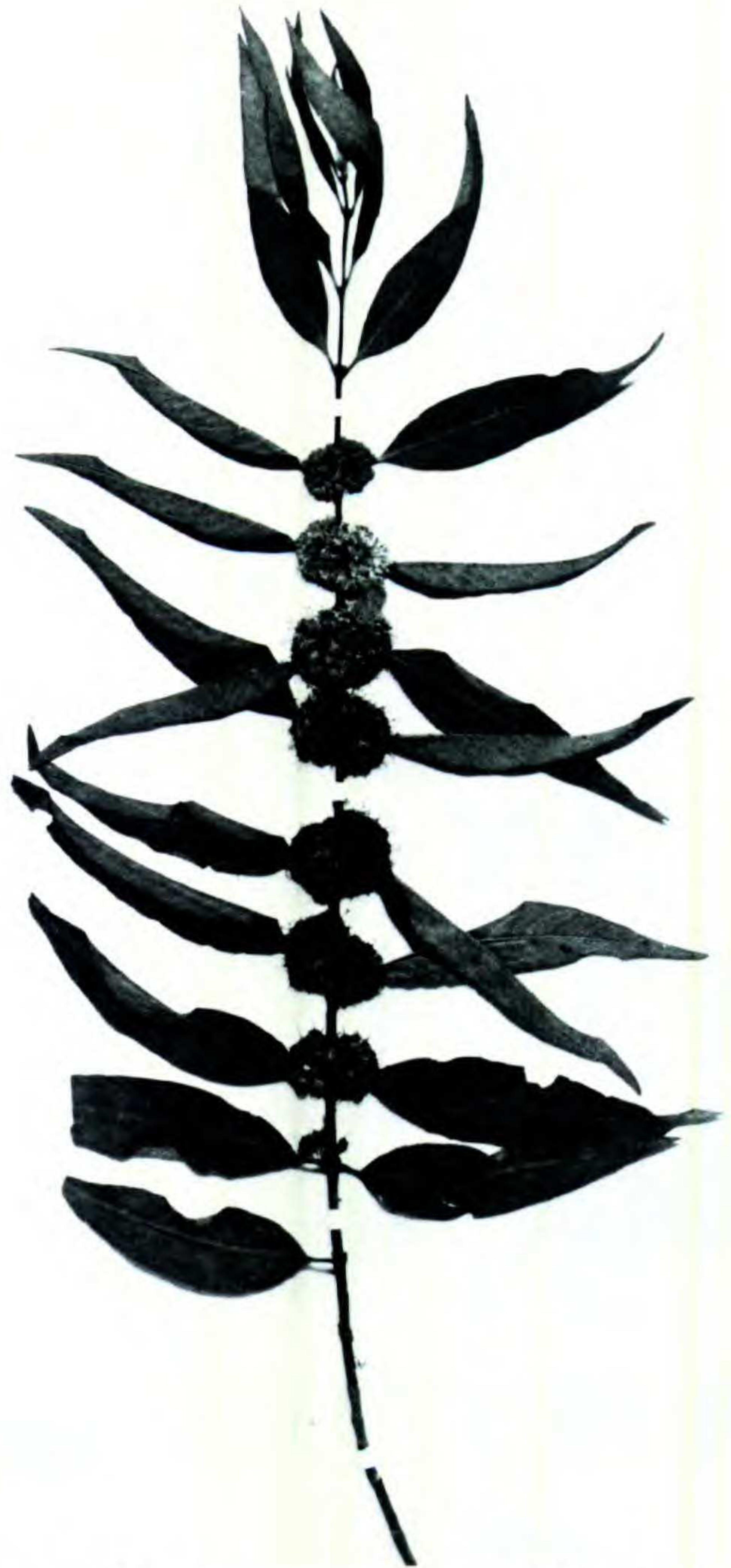


FIGURE 25. *Lythraceae*. *Adenaria floribunda*; flowering branch. (Bolivia: Vic. Sorata, M. Bang 1311 (M).)

by Koehne (1883: 118) for the verticillate species of the genus that in each whorl the number of flowers equals the number of leaves, i.e., the axil of each leaf bears a single flower. In *R. wallichii* (Fig. 26 II), however, the proximal verticils of a florescence comprising six or seven leaves bear only two or three flowers. The number of flowers increases distally, until each leaf axil of a verticil bears a flower. The disposition of the flowers in the lower whorls can be quite different, without any obvious rule. During the development of a shoot the number of leaves in the consec-

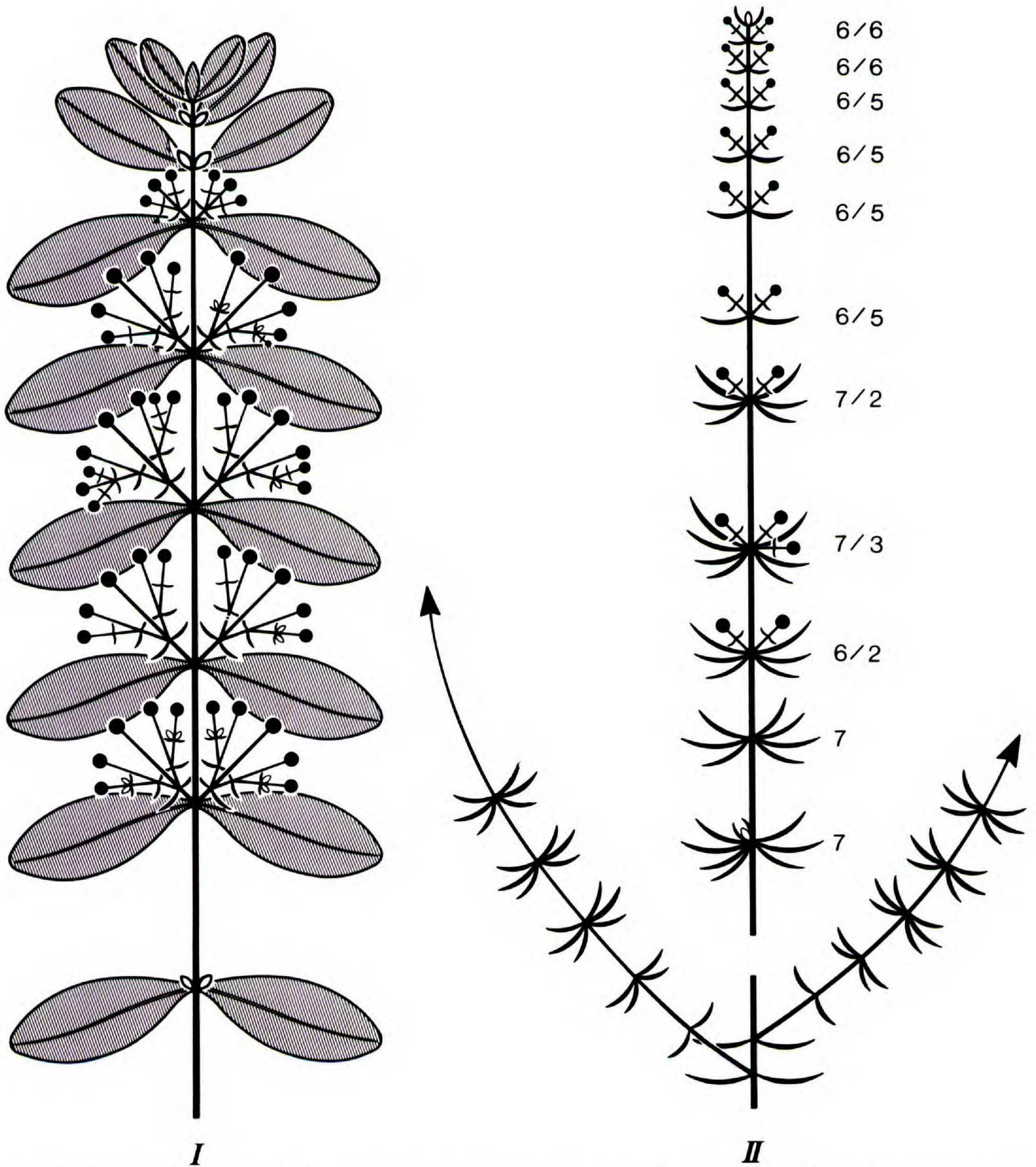


FIGURE 26. *Lythraceae*.—I. *Nesaea crassicaulis*; diagram of a flowering shoot.—II. *Rotala wallichii*; flowering branch. (For each verticil of the main axis the number of leaves and of axillary flowers is added.)

utive verticils increases gradually from two to four and six, then perhaps up to seven and decreasing to six again.

Among the taxa with copiously branched cymose partial florescences, the species of *Nesaea* sect. *Nesaea* (= sect. *Typonesaea* Koehne) subsect. *Tolypeuma* (E. Meyer) Koehne are remarkable. By shortening of the internodes of all consecutive ramifications the cymes are contracted to small headlike ag-

gregations of flowers enveloped by an involucre that is formed by the large cordate-lanceolate prophylls. The corollae of the flowers rise slightly above the border of these prophylls, which often are somewhat whitish and violet-nerved basally. The hypopodia of the capitulate partial florescences are prolonged. Since the main axis of the thyrse florescences—the main florescence and the co-florescences—is anauxotelic, the flores-

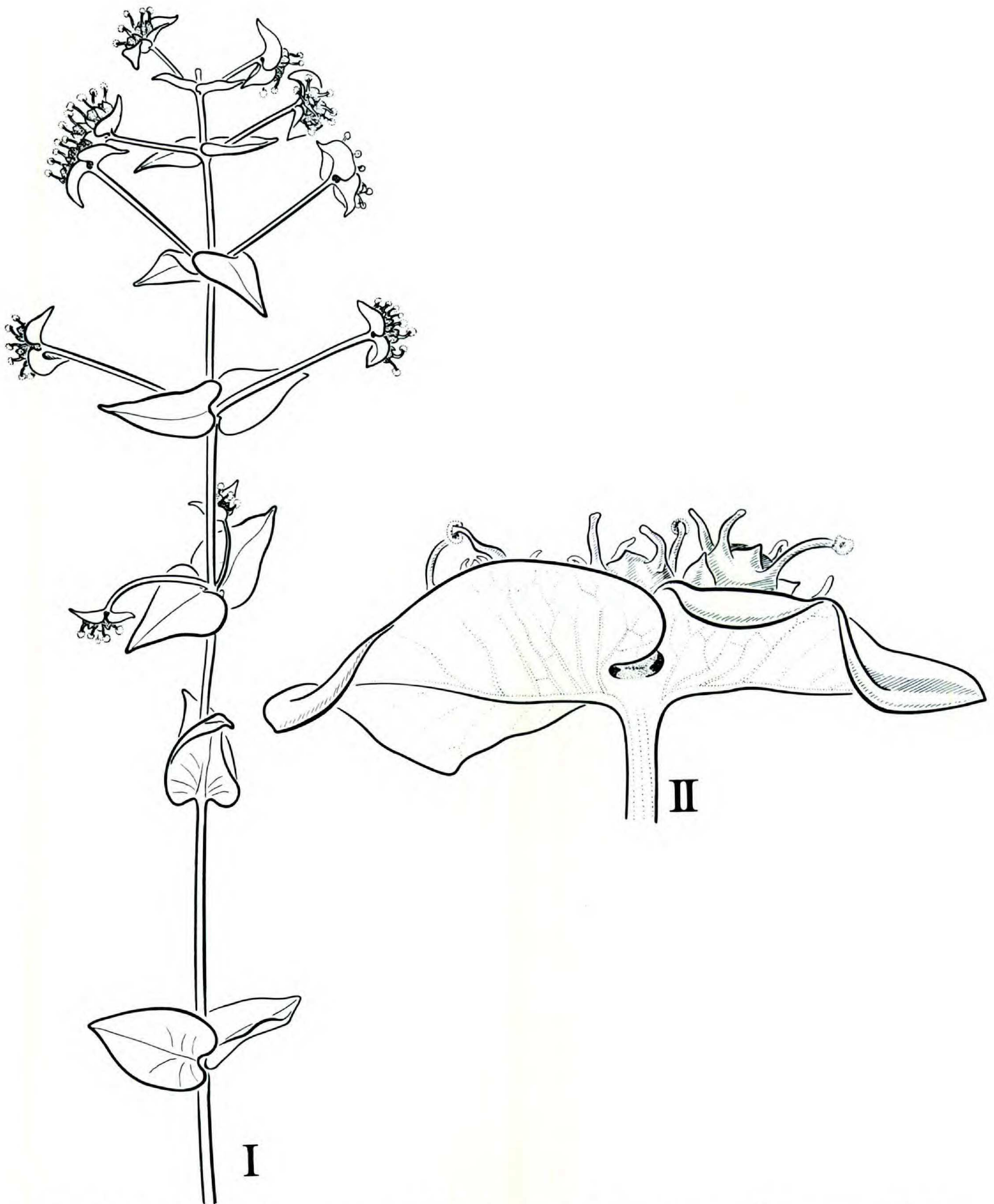


FIGURE 27. *Lythraceae*. *Nesaea erecta*.—I. Flowering plant.—II. Cymose partial florescence. (Rhodesia: Mapanza, E. A. Robinson 2839 (M).)

cences of these species, i.e., *Nesaea erecta* Guill. & Perr. (Fig. 27) or *N. cordata* Hiern, appear as botrytic systems composed of capitula.

In contrast to these species, the inflorescence of *Nesaea linearis* Hiern (sect. *Ty-*

ponesaea subsect. *Syntolypaea* Koehne) is described to form a terminal capitulum composed of "dichasia singula confertissima, sessilia, bracteolis superne dilatatis . . ." (Koehne, 1903: 223, 230, fig. 45C).

Likewise the lateral capitula of *Nesaea*

radicans Guill. & Perr. (also subsect. *Toly-peuma*), which are of similar appearance to those in *N. erecta* and *N. cordata*, are described to have four or six enlarged "prophylls," each of them subtending a small "dichasium" (Koehne, 1903: 8, 231). Indeed, these capitula proved to have a thyrselike ramification and to be provided with a terminal flower as Koehne had affirmed already. He did not investigate *N. linearis* in this respect. At least for *N. radicans*, however, it seems to be evident that the inflorescences are monotelic, as Koehne (1903: 8) affirmed with the statement that the inflorescences of *N. radicans* seem to form a transition to those of *Woodfordia*, *Lagerstroemia*, and *Lawsonia*.

A remarkable condensation of florescences is typical for *Pleurophora polyandra* Hook. & Arn. also; here, however, the florescences are spikes (Fig. 28 I, II).

As the treatment of inflorescences in the Lythraceae has shown already, the disposition for proliferation of inflorescences is widespread within this family. Proliferation takes place especially in frondose florescences, for example in *Heimia*, *Nesaea crassicaulis* (Fig. 26 I), *N. sagittifolia* Koehne, or *Adenaria floribunda* (Fig. 25).

Another factor responsible for the high degree of growth-form diversity of inflorescences, especially in herbaceous and suffruticose taxa, is the variation of the proportions between the different zones of the flowering plant, i.e., in polytelic taxa the main florescence, the enrichment zone, the inhibition zone, and, in perennials, the innovation zone.

Thus, Troll (1970: 92) reported that in *Diplusodon thymifolius* DC. the main florescence remains very small in comparison with the paracladial zone. The same seems to apply to *D. virgatus* Pohl, whereas in other species, e.g., *D. villosissimus* Pohl and *D. villosus* Pohl, we found the main florescence to be predominant, although the paracladial zone can be well developed too. The distal paracladia of these species had no hypotagma.

Of course, to a certain degree such differences as the unfolding of a smaller or greater

number of paracladia depend on the developmental stage of a plant and on environmental circumstances. The latter especially applies to annuals. Under severe environmental stresses such plants can be highly reduced and develop reduced inflorescences only, as Troll (1964: 363–364) described for *Ammannia coccinea* Rottb. The original plant depicted by Troll is presented here in a photograph (Fig. 28 IV). Probably the plant investigated and figured by Troll is not *Ammannia coccinea* but *A. latifolia* L.; the same then applies to Figure 28 IV. The hypotagma is reduced to two nodes. Only the uppermost of them bears paracladia, while the paracladia in the axils of the cotyledons remain undeveloped. The largest part of the plant is formed by the frondose proliferating florescence with many triadic partial florescences. In reduced plants of *Pleurophora polyandra* the inflorescence frequently only consists of a short headlike spike that is preceded by the cotyledons and two pairs of foliaceous leaves with paracladia absent from their axils (Fig. 28 I). In other individuals, more or less vigorous paracladia ending in a florescence can develop from the axils of the cotyledons and/or from the axils of the following leaf pairs (Fig. 28 II). In *P. pusilla* Hook. & Arn. the reduction of ramification seems to be a constituted character.

By dense sowing of *Lythrum hyssopifolia* L., plants without any paracladia were obtained by Troll (posthumous notices), whereas in normal plants the paracladial zone is well developed.

The frequent occurrence of accessory buds that develop as single flowers or vegetative or flower-bearing branches has been mentioned already. With the exception of *Cuphea* (Eichler, 1878b: 479), there is scarcely a genus of Lythraceae in which they are completely missing. Since Koehne (1873: 112) has given a survey of the various forms and their distribution within the family, we can confine ourselves to the treatment of the genus *Lythrum*, in which the occurrence of accessory flowers is very important for the appearance of the inflorescences.

In *Lythrum* the florescences of subgen. *Lythrum* (= *Salicaria* Koehne) and of sect. *Mesolythrum* Koehne of subgen. *Hyssopifolia* are spikes or botrya.

A flowering individual of *Lythrum salicaria* L. (Fig. 29 II, III) shows a clear zonation: the frondulose main florescence, a paracladial zone (enrichment zone) in which the paracladia are still unfolding, and an inhibition zone below the paracladial zone. Since *Lythrum salicaria* is a perennial, the inhibition zone is preceded by an innovation zone at the base of the plant. According to Troll (posthumous notices), *L. salicaria* is a subshrub rather than a perennial herb since the primary axis as well as the primary root shows intense lignification, as in *Hypericum perforatum*. In young plants (Fig. 29 I) a favored development of the axillary buds of the cotyledons (cotyledonary shoots) and of the next basal leaf pair can be seen. The cotyledonary shoots can develop branches from the axils of their prophylls at early stages, and a phylloscopic accessory bud can arise in the axils of the cotyledons. In vigorous plants the paracladial zone can be considerably expanded, and the paracladia can develop second-order paracladia. In the basal part of the flowering zone the phyllotaxis changes from decussate to alternate (Wydler, 1860: 238; for the phyllotaxis of *L. virgatum* and *L. hyssopifolia* see Wydler, 1872: 254). The florescences are thyrses, however exceedingly modified by the formation of phylloscopic accessory cymes or flowers (Roepert, 1826: 109).

Eichler (1878b: 479) observed that below the cymose partial florescence there are mostly two accessory three-flowered cymes (Fig. 30 IIa), the lower of which is often rudimentary. There is an additional accessory flower below each of the lateral (secondary) flowers of the primary partial florescence. These additional flowers bear prophylls as do the regular lateral (secondary) flowers of the cyme. Thus a transversal series of five flowers results, below which there is a three-flowered cyme still provided with prophylls of first order, and below this another one of rudimentary flowers without prophylls. *Lythrum pur-*

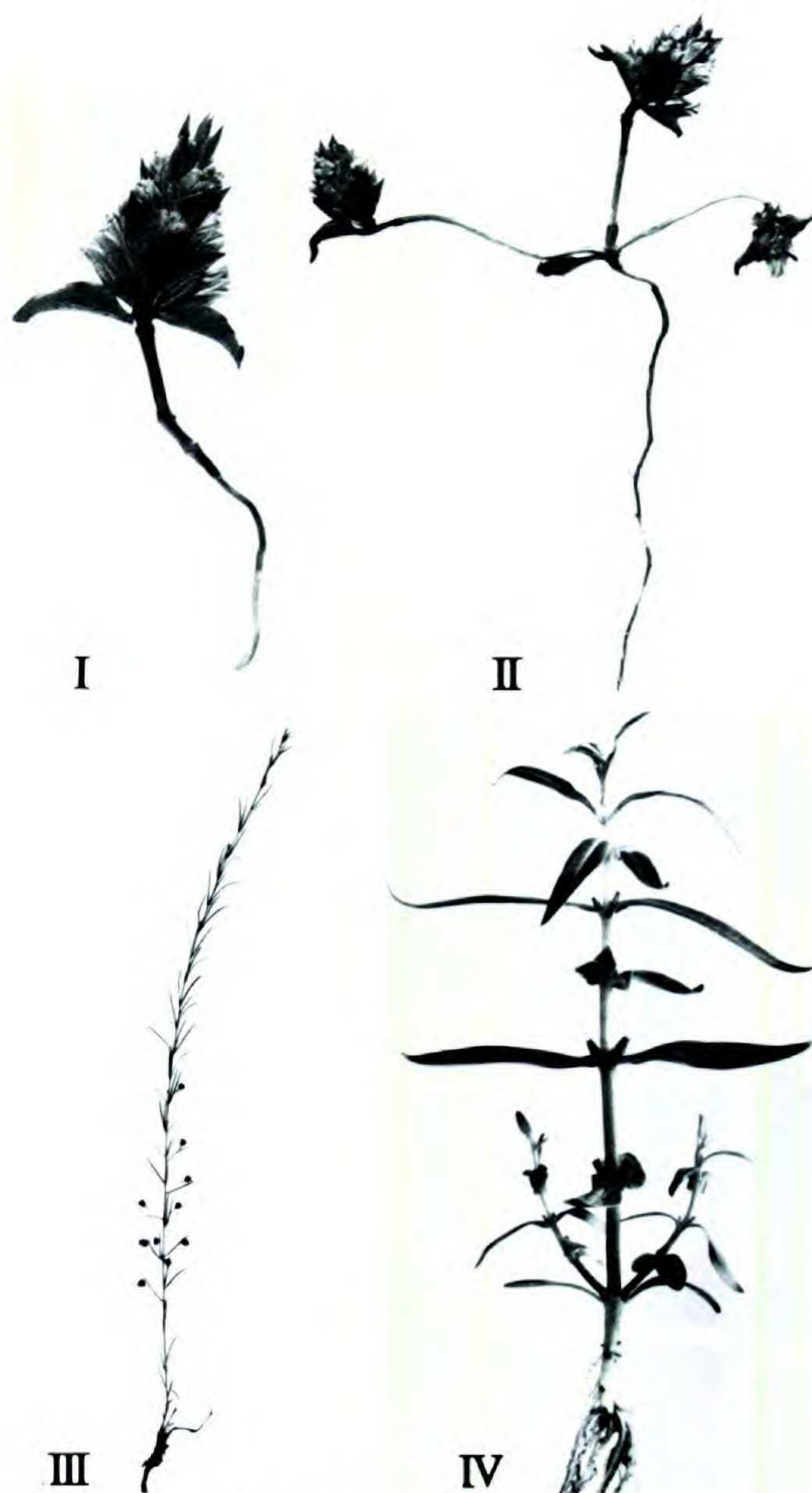


FIGURE 28. *Lythraceae*.—I, II. *Pleurophora polyantra*; reduced form (I) and plant with well-developed basal paracladia (II).—III. *Nesaea linifolia*; flowering individual.—IV. *Ammannia coccinea*; reduced individual. (Photographs III and IV from Troll.)

shianum Steudel is reported to be similar in this respect (Fig. 30 IIb).

Troll (posthumous notices), however, found triadic flower groups in place of the singular accessory flowers that accompany the secondary flowers of the regular partial florescence (Fig. 30 Ia). He also noted that there may be one (as_1) or two (as_1, as_2) accessory cymes. In the latter case the as_1 bears single accessory flowers in the axils of its prophylls, and the as_2 likewise is provided with prophylls (Fig. 30 Ic).

In all partial florescences, anthesis of the primary flower takes place first, followed by the secondary flowers, then the primary flow-

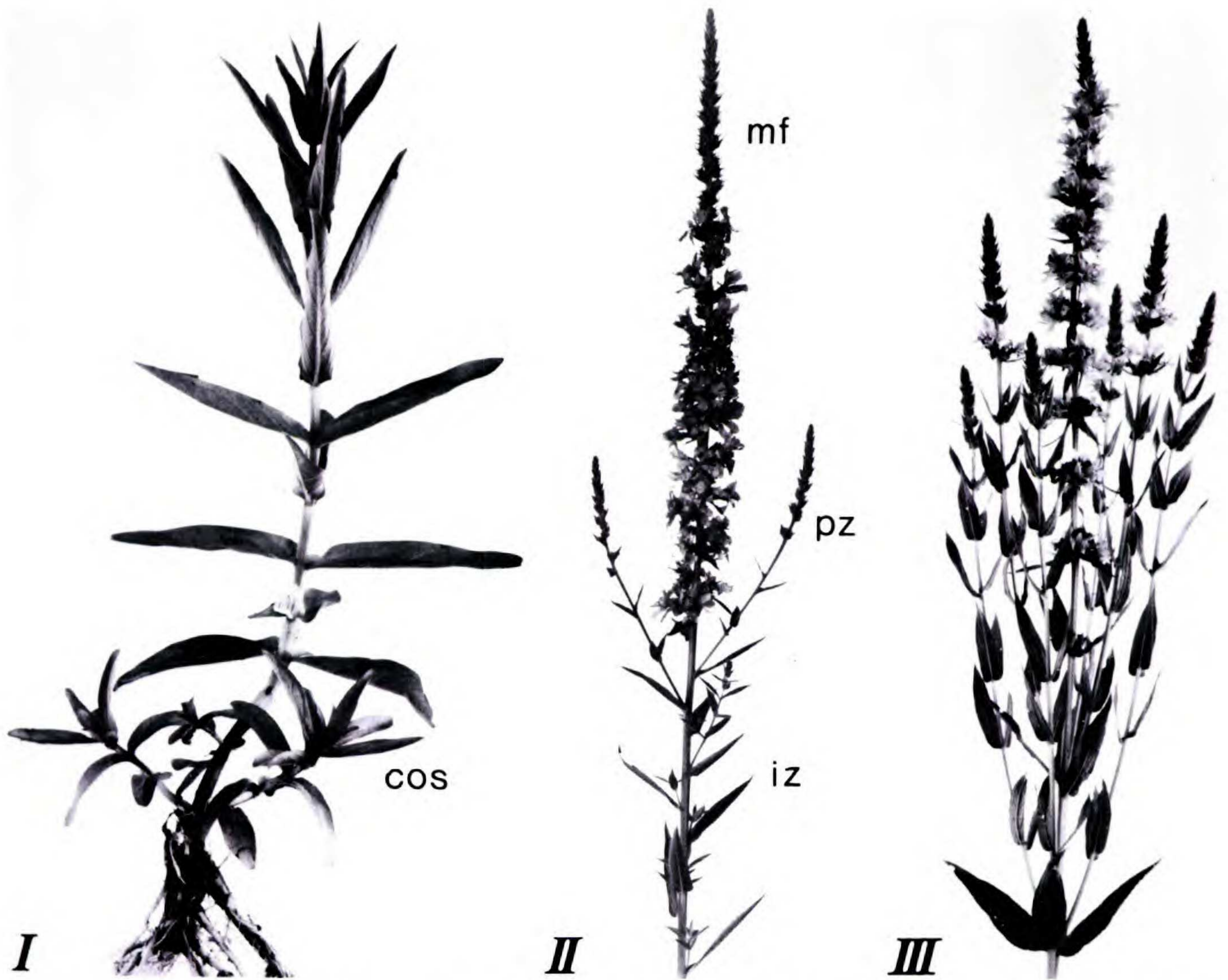


FIGURE 29. *Lythraceae*. *Lythrum salicaria* L.—I. Young plant with favored development of the cotyledonary shoots (*cos*) and a second pair of basal branches.—II. Flowering individual with large main florescence (*mf*), enrichment zone (paracladial zone, *pz*), and inhibition zone (*iz*).—III. Plant with trimerous leaf whorls and expanded paracladial zone. (Photographs from Troll.)

ers of the as_1 , and so forth. As a consequence, the efflorescence of the whole florescence is progressing from base to top repeatedly “as in *Verbascum*” (Wydler, 1843: 184, 1851a: 370–371). According to Wydler (1860: 240), who referred to Koch, it is not rare to have a vegetative accessory bud below the single flowers of the spicate florescence.

Koehne (1903: 6) reported that in *Lythrum tribracteatum* Salzm. and some other species the accessory branch forms a short, dense botrytic florescence.

By *recaulescent* shifting, the place of attachment of the subtending leaves (perophylls) can be relocated onto the pedicels of the flowers, which in reality originate from the axils of the perophylls. Thus these can be situated just below the flower. Examples can be found in *Rotala* and *Decodon*.

In most species of *Cuphea*, the attachment of the flowers within the botrytic florescences is modified by the coalescence of their pedicels with the main axis up to the next node (Hochstetter, 1850: 182; Wydler, 1851a: 371, 1861; Eichler, 1878b: 478 ff.). This sort of concrescence is well known as *concaulescence*. In *C. nitidula* Kunth, *C. appendiculata* Benth., and some other species (cf. Koehne, 1883: 119), the flowers are mostly still in normal axillary position. In the case that both axils of the decussate leaves are fertile (“*Cupheae oppositiflorae*”), the pedicels of both flowers are attached to the main axis up to the next node (Fig. 31). Thus the flowers and prophylls attached between the insertion of the leaves (or somewhat below) really originate from the leaf axils of the preceding node. In “*C. oppositiflorae*” even the

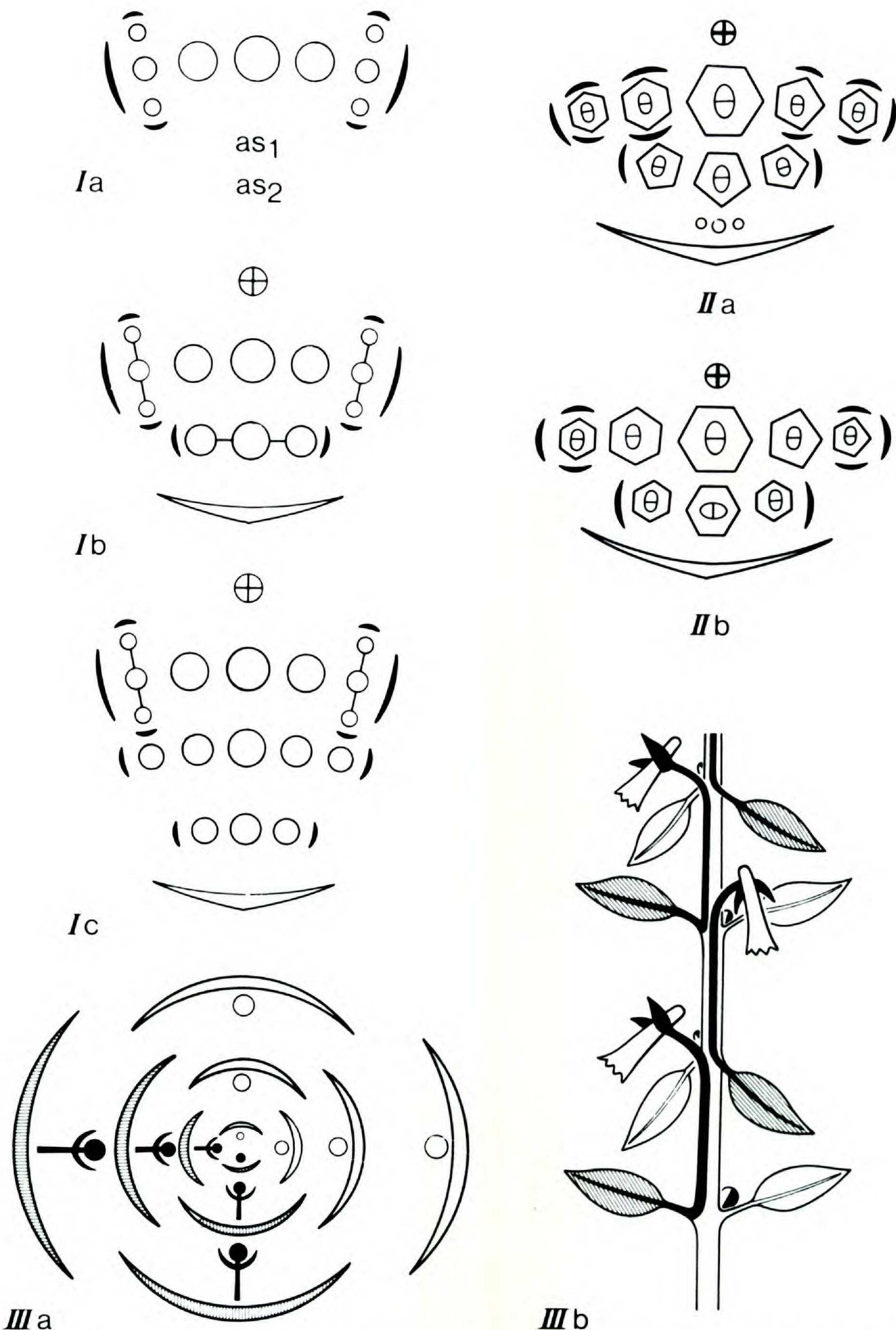


FIGURE 30. *Lythraceae*.—I, II. Partial florescences and accessory flowering branches (as_1 , as_2) of *Lythrum salicaria* in diagrams according to Troll (Ia–c) and Eichler, and of *L. purshianum* according to Eichler (IIb).—III. Horizontal (IIIa) and vertical (IIIb) projections of ramification in alternatiflorous *Cuphea latifolia* after Eichler (slightly modified).

initially vegetative branches show a slight concaulescence (Koehne, 1873: 111). In the case that only one leaf axil of a node is fertile (*C. alterniflorae*), there is only one flower at-

tached at the flanks of the next node. The bud situated in the second axil of the opposite leaves remains within the axil. Since the fertile axil of the third node always is placed above



FIGURE 31. *Lythraceae*.—*Top, left.* *Cuphea latifolia*; plant at the beginning of flowering.—*Top, right.* *C. procumbens*; florescence.—*Bottom.* *C. micropetala*; florescence (*left*), and detail (*right*). (Photographs from Troll.)

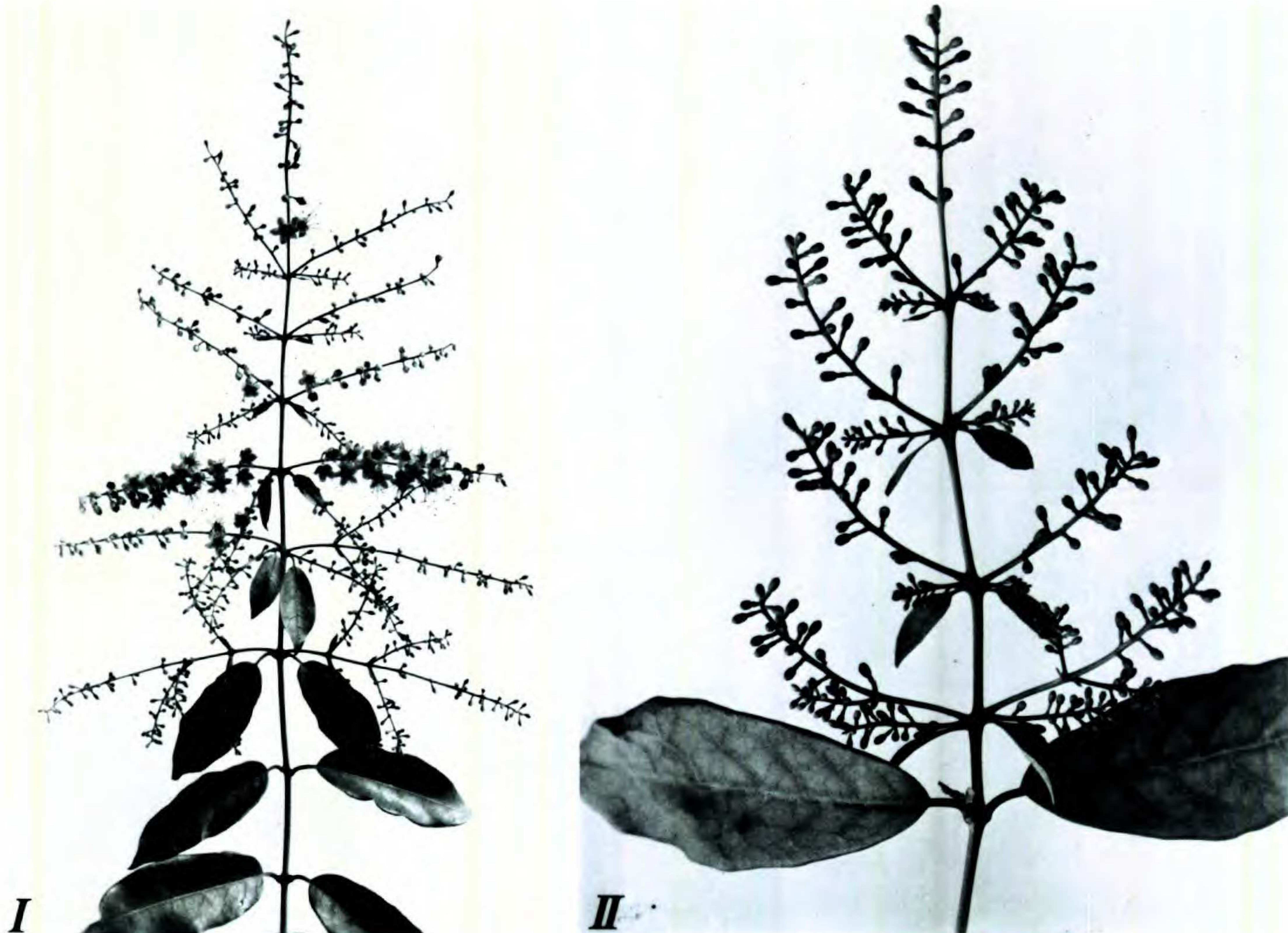


FIGURE 32. *Combretaceae*. *Combretum coccineum*; flowering branches in anthesis (I) and before anthesis (II). (Photographs from Troll.)

the fertile axil of the first, and the fourth always is superposed to the fertile axil of the second node (Fig. 30 IIIb), the result is two vertical rows of flowers diverging by 90° (just as two vertical rows of axillary buds, Fig. 30 IIIa).

The ligneous genus *Rhynchochalyx* Oliv., formerly included in Lythraceae and now regarded to represent a separate family, has monotelic inflorescences. In *R. lawsonioides* Oliv., the inflorescence forms a bracteose thyrsopaniculate system at the end of leafy shoots. At the bases of the paracladia uniflorous or triflorous accessory branches can be found.

The monotypic genus *Alzatea*, which is now regarded to form a separate family, has diplothyrsoidal inflorescences, probably of monotelic character. On the latter point some uncertainty remains because of the fragmentary state of the examined herbarium material of *A. verticillata* Ruiz & Pavón. The lowermost thyrsoidal paracladia are accompanied

by accessory branches that form thyrsoids too.

In the monotelic character of their conical dithyrsoidal inflorescences, *Rhynchochalyx* and *Alzatea* at least do not join the progressed members of the Lythraceae.

COMBRETACEAE

The inflorescences of Combretaceae are polytelic throughout. Although there are prophylls present in *Laguncularia*, *Lumnitzera*, and *Macropteranthes*, the inflorescences are nearly always spikes or rarely botrya.

The central type of inflorescence architecture within the family may be represented by *Combretum coccineum* (Sonn.) Lam. (Fig. 32 I). The leafy shoots terminate in a synflorescence composed of a botrytic main inflorescence at the top of the whole ramification system, preceded by several pairs of paracladia. Phyllotaxis is often not strictly decussate



FIGURE 33. *Combretaceae*. *Combretum coccineum*.—I. Mode of effloration.—II. Detail. (Photographs from Troll.)

within the family. Besides *Terminalia*, seven genera are reported to have alternate leaves, though in many cases they are subdecussate. In many climbers only the distal branches show decussate leaves. In *Terminalia*, *Bucida*, *Buchenavia*, *Ramatuela*, *Anogeissus*, *Finetia*, *Conocarpus*, and *Lumnitzera*, the leaves are spiral. The four distal pairs of paracladia are confined to their (co-)florescences, whereas the two proximal pairs bear two or four pairs of second-order paracladia, which are likewise limited to their (co-)florescences. In descriptive terms the ramification can be classified as a heterothetic triplobotryum. The foliation in the proximal part of the main axis is frondose but quickly changes over to bracteose; the flower-bearing twigs only develop small bracts. As shown by Figure 33 I, II, the efflorescence progresses from base to top in the sequence of the paracladia (I) as well as in the paracladia themselves (II); in this course the main florescence gains a slight lead in comparison with the preceding paracladia. Figure 33 II also shows that all flowers of the florescences, even those of plagiotropic ori-

entation, are turned upwards, a typical feature of many species, which has led to the popular name "cepillo de mono" (monkey's brush). This name especially applies to *C. fruticosum* (Loefl.) Stuntz (*C. secundum* Jacq., Fig. 34), in which the paracladia are poorly developed in favor of the vigorous development of the dense-flowered main florescence. In Figure 32 II, each of the first-order paracladia is accompanied by an accessory branch bearing a botrytic florescence. This is typical of many *Combretaceae*.

Synflorescences similar to those described here for *Combretum coccineum* can be found in various taxa of the family, such as *Laguncularia racemosa* (L.) Gaertner, *Thiloa glaucocarpa* (Martius) Eichler, *Calycopteris floribunda* (Roxb.) Lam., *Meiostemon tetrandrus* (Exell) Exell & Stace (cf. table I in Exell & Stace, 1966), *Campylogyne* Welw. ex Hemsley (the florescences with showy bracts), species of *Buchenavia* and *Terminalia* (*T. tomentosa* Bedd.; *T. paniculata* Roth, see also Sell, 1982, fig. 10a; *T. citrina* (Gaertner) Roxb. ex Fleming; *T. chebula* Retz., cf. Brandis, 1893, fig. 55), and in *Quisqualis*. In *Q. indica* L., the inflorescence can consist of a spicate main florescence terminating leafy twigs, contrasting with them by its bracteous foliation. The main florescence, however, can be accompanied by one or two pairs of paracladia originating from the axils of the foliaceous leaf pairs preceding the main florescence. These paracladia usually bear one or two more or less foliaceous leaf pairs at their bases. Likewise, the lowermost leaf pair of the main florescence may be somewhat foliaceous. *Cacoucia coccinea* Aublet (*Combretum cacoucia* (Ball.) Exell) seems to be characterized by developing only a long voluminous main florescence (Fig. 35). The same applies to some other species formerly included in this genus (*Cacoucia splendens* Hemsl. = *Combretum bracteatum* (Laws. pro parte) Engl. & Diels, *Cacoucia paniculata* Laws.).

Lumnitzera coccinea and *L. racemosa* differ considerably in the position of their spicate florescences (see also Brandis, 1893). In *L.*

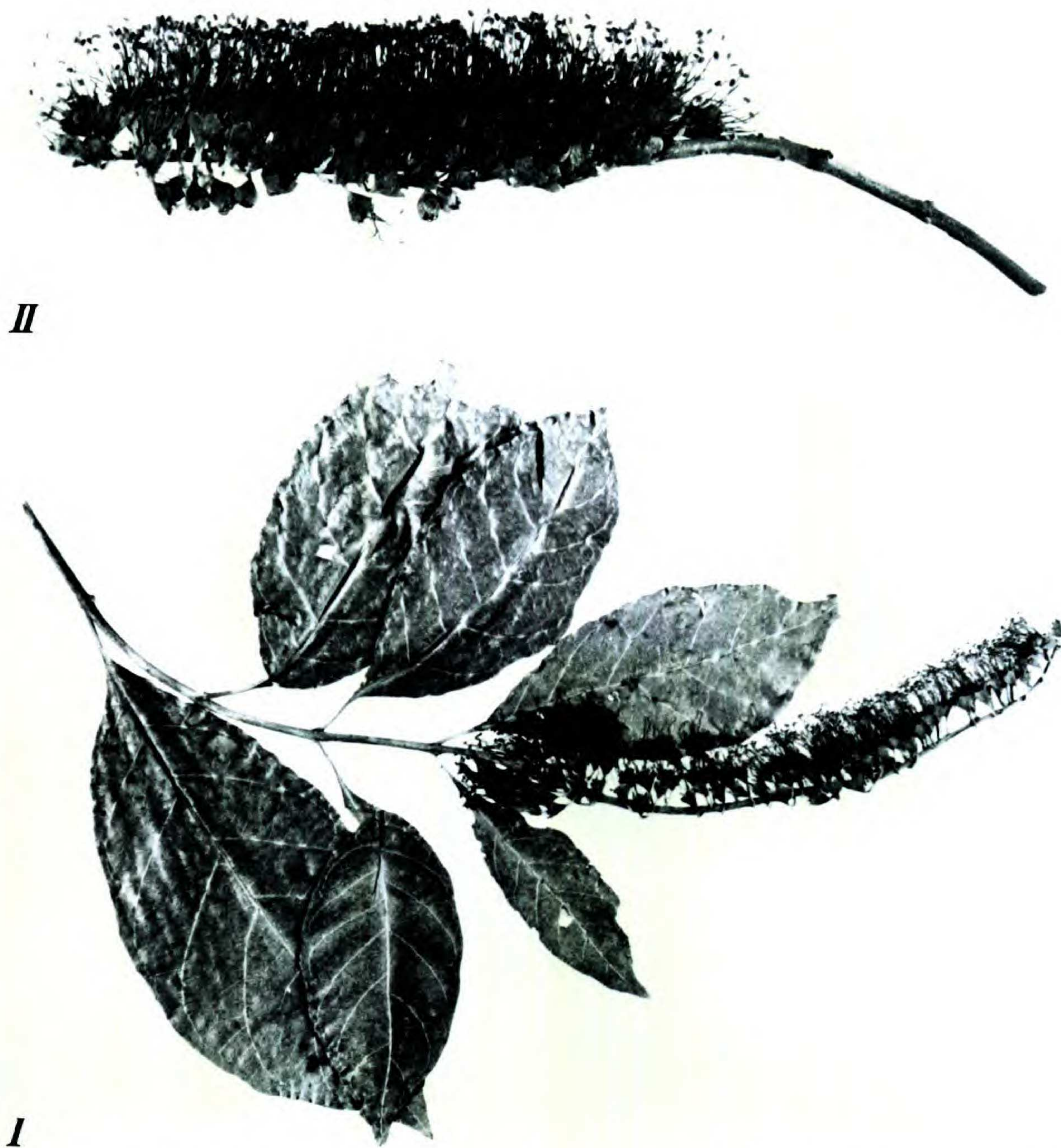


FIGURE 34. *Combretaceae*. *Combretum fruticosum* (= *C. secundum*); flowering branch (I) and botrytic inflorescence (II). (El Salvador: Weberling 164, 175.)

littorea (Jack) Voigt, normally a bracteose spicate main inflorescence terminates a leafy shoot, and paracladia are missing. In *L. racemosa* Willd., however, the syninflorescence consists of paracladia only, which form 10–20-flowered, long-peduncled spikes originating in the axils of foliaceous leaves of a leafy shoot with indeterminate growth. In *L. coccinea*, however, the foliaceous shoots that end in a spicate main inflorescence are not very large and represent branches of a shoot with indeterminate vegetative growth, too.

Within *Terminalia*, a great number, per-

haps the majority, of the species are characterized by leafy proliferating inflorescences. In some of these species the flowering branches grow with well-developed internodes, and after the production of several spicate paracladia which originate in the axils of foliaceous leaves, these branches return to vegetative growth. *Terminalia oblonga* (Ruiz & Pavón) Steudel serves as an example (see also *T. brownii* Fresen., Sell, 1982, fig. 10d). In other species the internodes of the main axis remain short within the flowering zone. Thus the leaves are “crowded at the ends of the



Cacoucia coccinea

FIGURE 35. *Combretaceae*. *Cacoucia coccinea* (from Aublet, J. B., *Hist. Pl. Guiane Franç.* III, pl. 179, 1775).

branches," and the synflorescence has a rosettelike shape. This applies to *T. catappa* L. (Fig. 36; for the crown form and branching pattern of *T. catappa* and *T. latifolia* see Fisher & Hibbs, 1982), *T. bellirica* (Gaertner) Roxb., *T. zollingeri* Exell, *T. sumatrana* Miq., *T. trivialis* Slooten, and many other species, also to *Bucida* L. In *T. gigantea* Slooten, which shows a similar architecture, the spicate paracladia are very long, with many loosely arranged flowers. In *T. australis* Camb., on the other hand, the paracladia bear a smaller number of densely aggregated flowers that form a long-peduncled head. The flowering branches of this species are brachyblastlike proliferating twigs with well-developed internodes. They develop from axillary buds of an older shoot but also arise from its terminal bud and later continue its growth. In *T. triflora* (Griseb.) Lillo, the brachyblasts, which bear several bud scales at their bases, remain very short, at least during the anthesis of their four to six paracladia, which likewise form few-flowered, long-peduncled heads.

Formation of flowers is limited to brachy-

blasts in many species of other genera. Thus in the species of *Pteleopsis* Engl., the flowering branches are brachyblasts originating from older macroblasts. They bear a few bud scales at their bases, some pairs of foliaceous leaves, and an umbel-shaped to botrytic main florescence, which in its proximal part can bear small foliaceous pherophylls. We could, however, also observe heterothetic diplobotrytic inflorescences with somewhat umbellate florescences in some specimens of *P. myrtifolia* (Lawson) Engl. & Diels.

In *Combretum salicifolium* E. Meyer, and in *C. apiculatum* Sonder (Fig. 37 I) brachyblastlike branches situated on macroblasts of the previous year bear simple paracladia in the axils of the two or three lowermost pairs of foliaceous leaves; these brachyblasts proliferate at the end of the anthesis of the paracladia (see also Brandis, 1893, fig. 59). *Combretum bracteosum* (Hochst.) Brandis is similar.

The florescences of *Combretum salicifolium* are contracted to 15–20-flowered head-like aggregations (see Brandis, 1893: 122, fig. 59A). The same applies to *C. erythrophyllum* (Burch.) Sonder (Fig. 37 II), in which the proliferating brachyblasts bear several pairs of long-peduncled globose umbels arising from the axils of foliaceous leaves. Capitulum-like florescences are also reported, for example in *C. punctatum* Bl. (van Slooten, 1922), whereas in *C. apiculatum* Sonder the axillary florescences are spicate (Fig. 37 I).

Capitulate and very densely flowered, long-peduncled florescences can also be found in *Guiera senegalensis* Lam. and in species of *Buchenavia*, *Finetia*, and *Anogeissus*. In *Buchenavia capitata* (Vahl) Eichl. and *B. ochroprumna* Eichl., the paracladia bearing globose, ca. 20-flowered heads were observed on terminal rosette-shaped proliferating brachyblasts. They were inserted here at the base of the brachyblasts, thus preceding the leaf rosette. In contrast to these species, the floral zone of the brachyblasts in *B. kleinii* Exell succeeds the leaf rosette, and the inflorescences are ovoid. In some other species the paracladia bear loosely flowered spikes and are inserted at the top of the brachyblasts

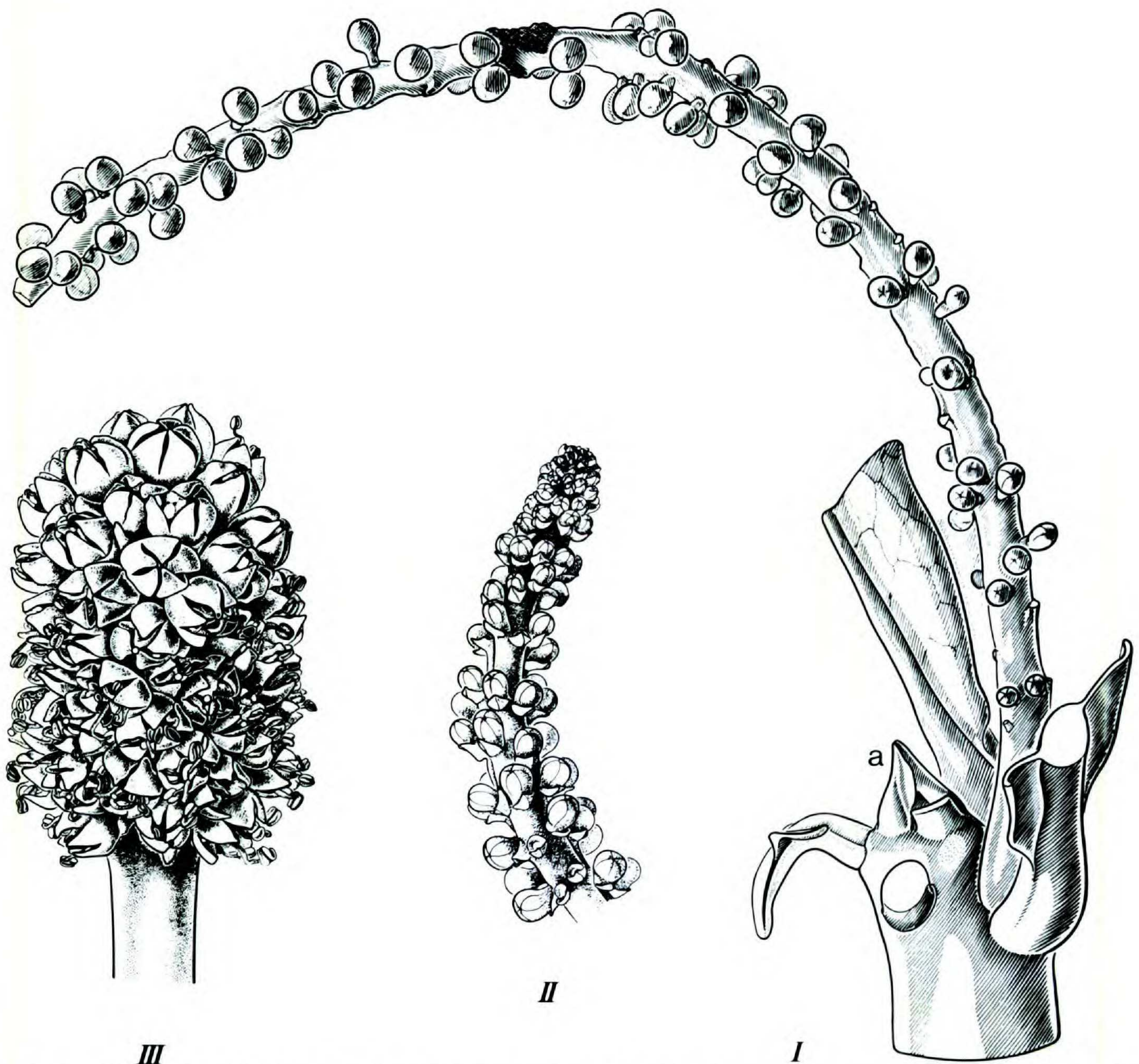


FIGURE 36. *Combretaceae*. I, II. *Terminalia catappa*.—I. Proliferating inflorescence with one spikelike paracladium, the leaves partly removed; apex (a) of the main axis.—II. Distal part of a paracladium.—III. *Conocarpus erecta*; capitulate paracladium.

more or less following the leafy zone (*B. macrophylla* Eichl., *B. suaveolens* Eichl.) or at the base of the brachyblasts, preceding the rosette (*B. oxycarpa* (Martius) Eichl.).

In *Anogeissus acuminata* (Roxb. ex DC.) Wall. ex Bedd. and *A. latifolia* (Roxb. ex DC.) Wall. ex Bedd., the synflorescences consist of a globose main florescence and an enrichment zone comprising several paracladia, each originating in the axil of a foliaceous leaf and bearing a globose co-florescence on a long peduncle. The paracladia can be accompanied by similar-shaped accessory branches.

In *Conocarpus erecta* L. (Fig. 38) the inflorescence terminating a leafy shoot is com-

posed of one terminal and many lateral, short-peduncled, ovoid capitula, which together form a heterothetic botrytic or diplobotrytic system. The basal leaves within this system are foliaceous, diminishing distally, and ultimately convert to small bracts. At least in the distal part of the inflorescence the paracladia are accompanied by accessory branches forming particular peduncled capitula.

In general the tendency to form condensed inflorescences is not very strong within the *Combretaceae*. Exell (1962), however, saw some evolutionary consequences resulting from a conflict between pollination strategies and the development of winged fruits of "massed flowers" that might cause "space



FIGURE 37. *Combretaceae. Brachyblasts.*—I. *Combretum apiculatum*. (SW Africa, Windhoek, R. Seydel 3666 (M).) —II. *C. erythrophyllum*. (South Africa, Cape Prov.: King Williams Town, D. M. Comens 1715 (M).)

problems.” The problem, however, seems to be more complex and needs empirical treatment with regard to flower biology as well as to carpology and chorology.

PENAEACEAE

The inflorescences of Penaeaceae were carefully investigated in the monographic work of Dahlgren (1967a–c, 1968, 1971). The basic type of ramification is a thyrsoid (a thyse with a terminal flower) as in *Sonderothamnus petraeus* (Barker) Dahlgren (Fig. 39 II) and *S. speciosus* (Sonder) Dahlgren. In the majority of taxa the cymose (triadic) paracladia are reduced to their primary flower. The thyrsoid thus is converted to a stachyoid as presented by *Saltera sarcocolla* (L.) Bullock (Figs. 39 I, 41 II, 42 I).

A peculiarity of the *Saltera* inflorescence is that the terminal flower is preceded by two pairs of pale membranaceous bracts. The low-

er bracts are narrow but broaden distally to an emarginate end; the next pair is much narrower, nearly linear, but also broadens to a truncate or slightly emarginate end. Two or three of the preceding leaf pairs bear single flowers in their axils, each of them with a pair of linear-spathulate prophylls. Since these prophylls are similar in shape to the upper pair of bracteoles preceding the flower that terminates the whole inflorescence, one could wonder if this flower is terminal or lateral. Dahlgren (1968), however, reported that the inflorescence can be reduced so far that the terminal flower is the only one remaining (Fig. 43 II). This, together with the comparison with the structure of inflorescences in some related taxa, particularly that of *Stylapterus fruticosus* (L. f.) A. Juss. (Figs. 40 II, 41 IV), confirms that there is a true terminal flower.

In some other taxa the terminal flower is

sometimes facultatively lacking or missing in all specimens. Thus in *Glischrocolla formosa* (Thunb.) R. Dahlgren the "inflorescence apex generally bears a terminal flower, but this may drop in an early stage" (Dahlgren, 1967b).

The inflorescences of *Brachysiphon rupestris* Sonder and *B. mundii* Sonder still have a terminal flower, whereas *B. fucatus* (L.) Gilg and *B. acutus* (Thunb.) A. Juss. have indeterminate spikes. In such cases the "apex ends in some scalelike leaves" (*B. fucatus*) or "as a dry tip" (Dahlgren, 1968). In *B. fucatus* (Fig. 39 IV), however, all the paracladia end in a terminal flower, and this refers not only to paracladia that are provided with the pair of prophylls only (and therefore otherwise could be interpreted as partial florescences of a polytelic thyse), but also to the lower paracladia with three or more leaf pairs. With some alterations the same applies to *Brachysiphon acutus*. Consequently we have to interpret these inflorescences as truncate monotelic systems.

In *Stylapterus* the inflorescence is "generally indeterminate, the apical tip being degenerated and dry, but in *S. fruticosus* and *S. ericifolius* it often ends with a terminal flower" (Dahlgren, 1967a). The semidiagrammatic figures of "selected rich-flowered inflorescences" of both species (Fig. 40) show that there is a strong tendency to reduce the number of flowers in the paracladia to their terminal flower. Particularly in *S. fruticosus* the result of this reduction is that the terminal flower of the whole ramification system as well as the terminal flower of the paracladia are preceded by two or three pairs of sterile leaves (see also Fig. 41 IV). This is in good concordance with the occurrence of two pairs of sterile bracts below the terminal flower of the *Saltera* inflorescence (Fig. 39 I). We also should note that the flowering system of *Stylapterus fruticosus* has a secondary inhibition zone below the terminal flower in addition to the primary inhibition zone that commonly precedes the paracladial zone.

Dahlgren (1971) described the inflorescence of *Penaea acutifolia* A. Juss. as "gen-

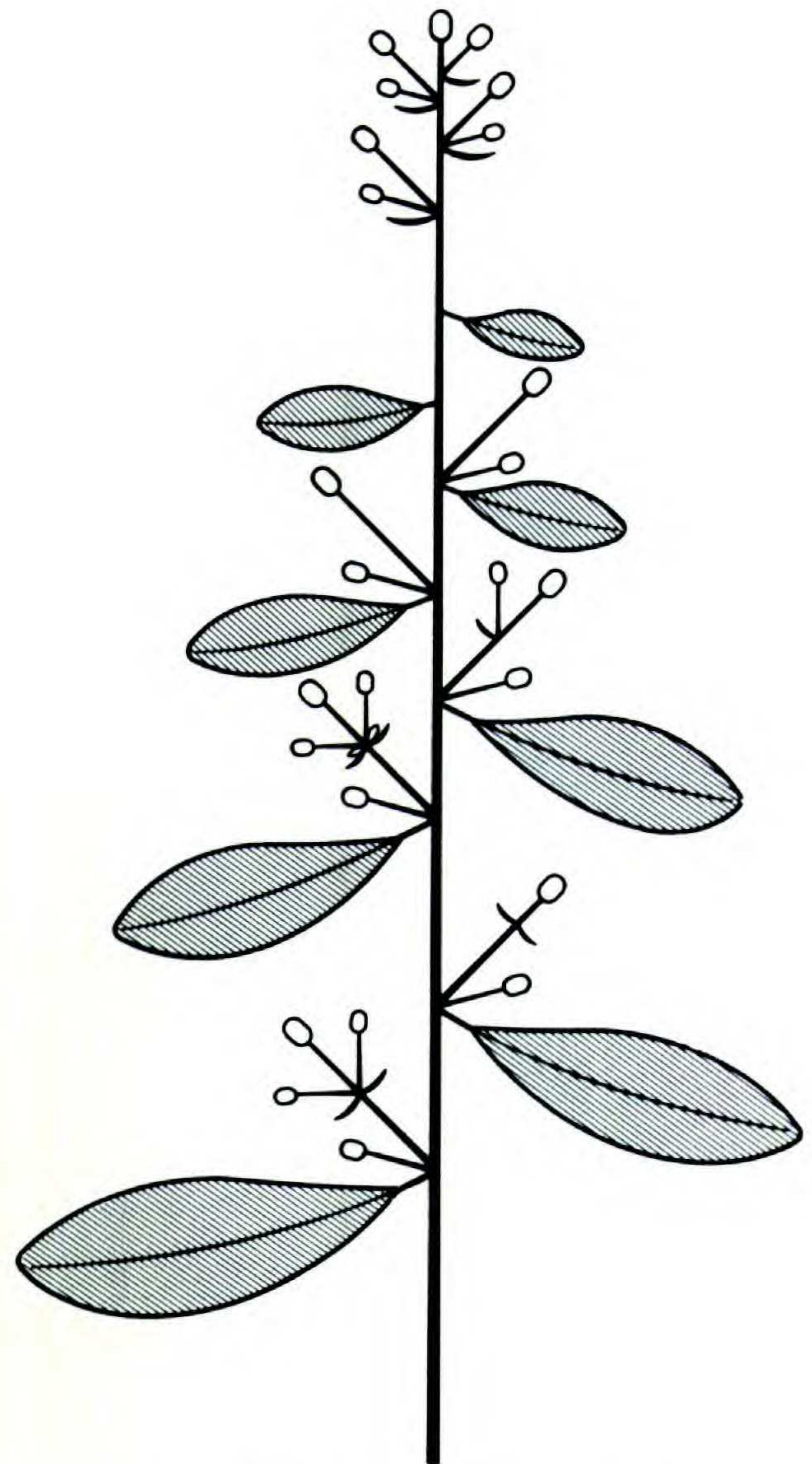
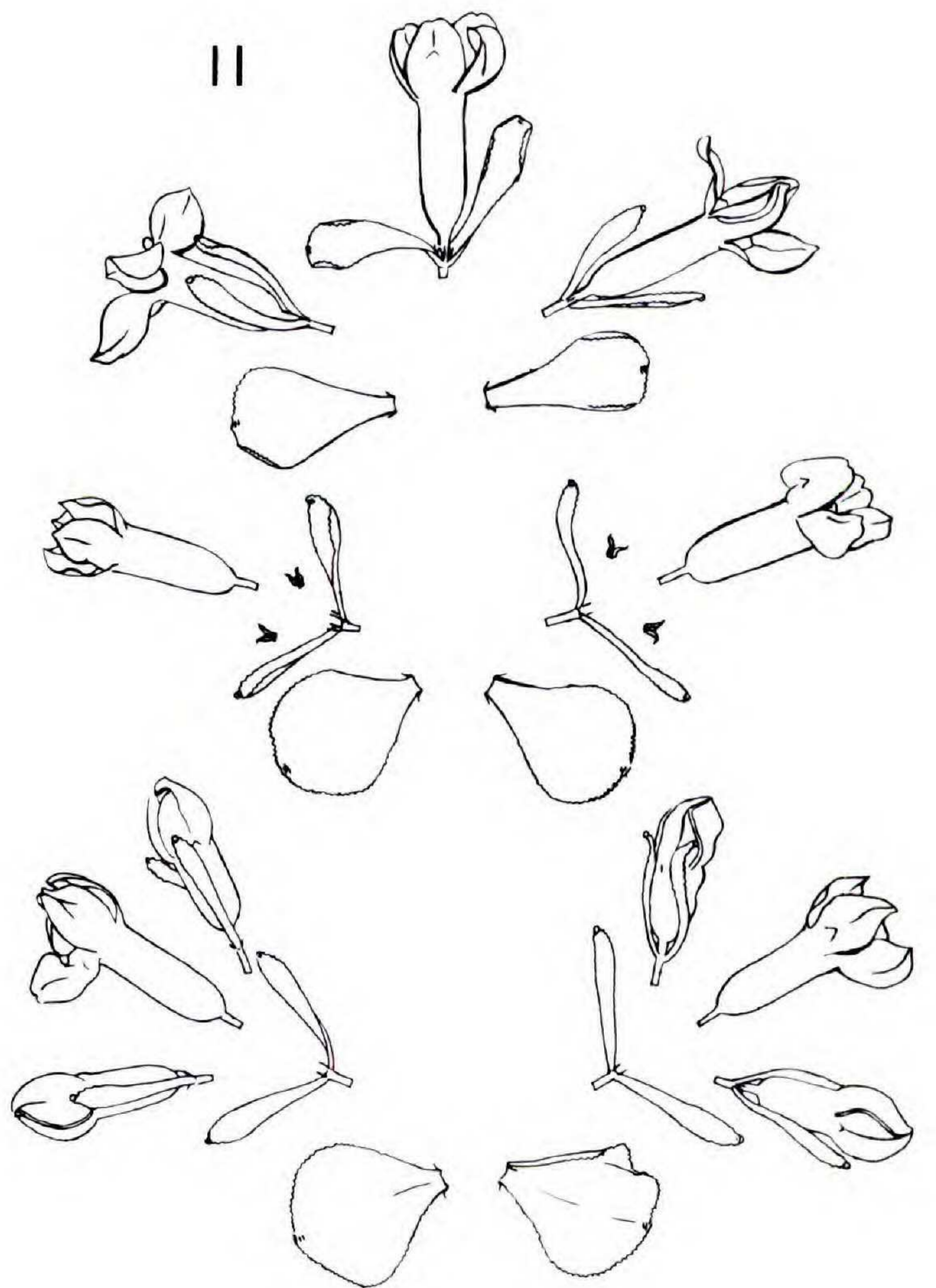
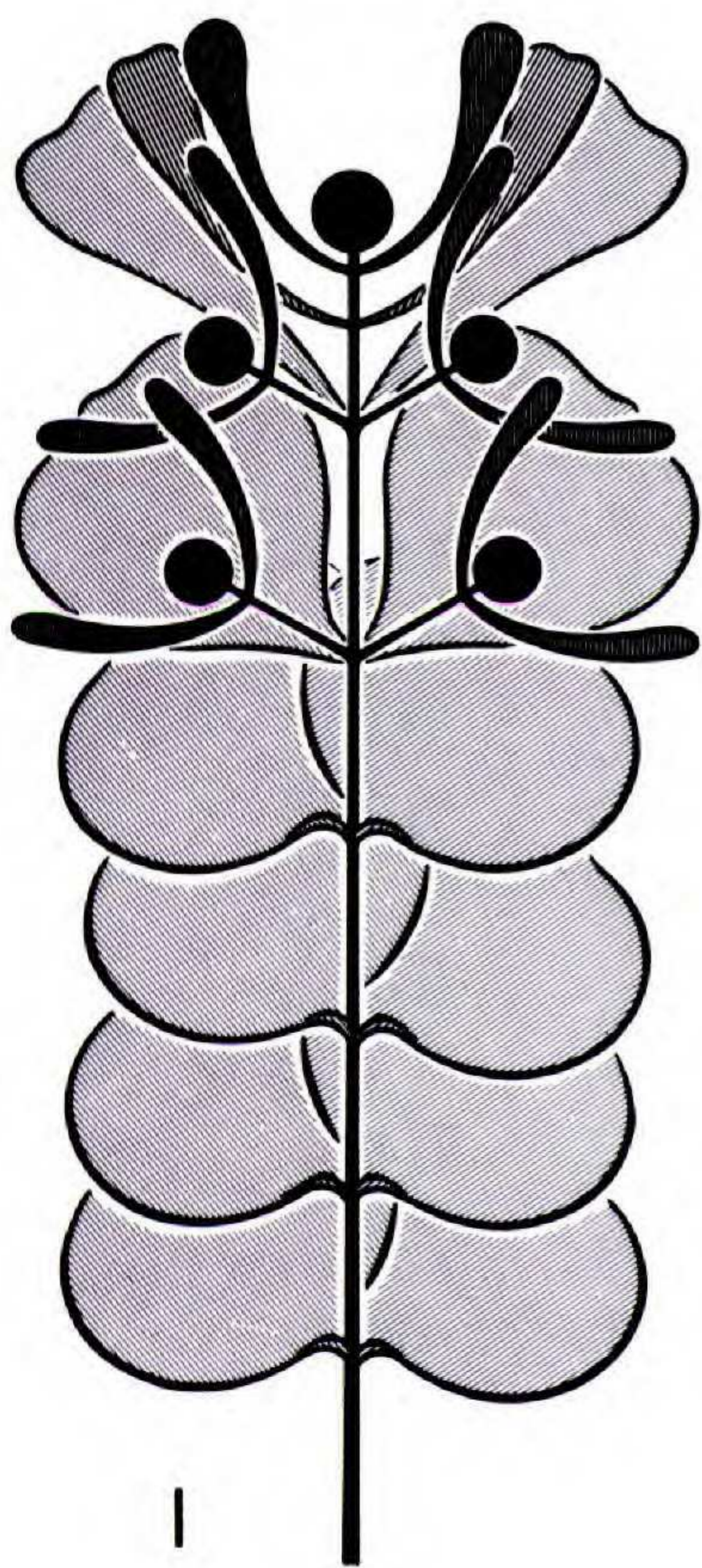
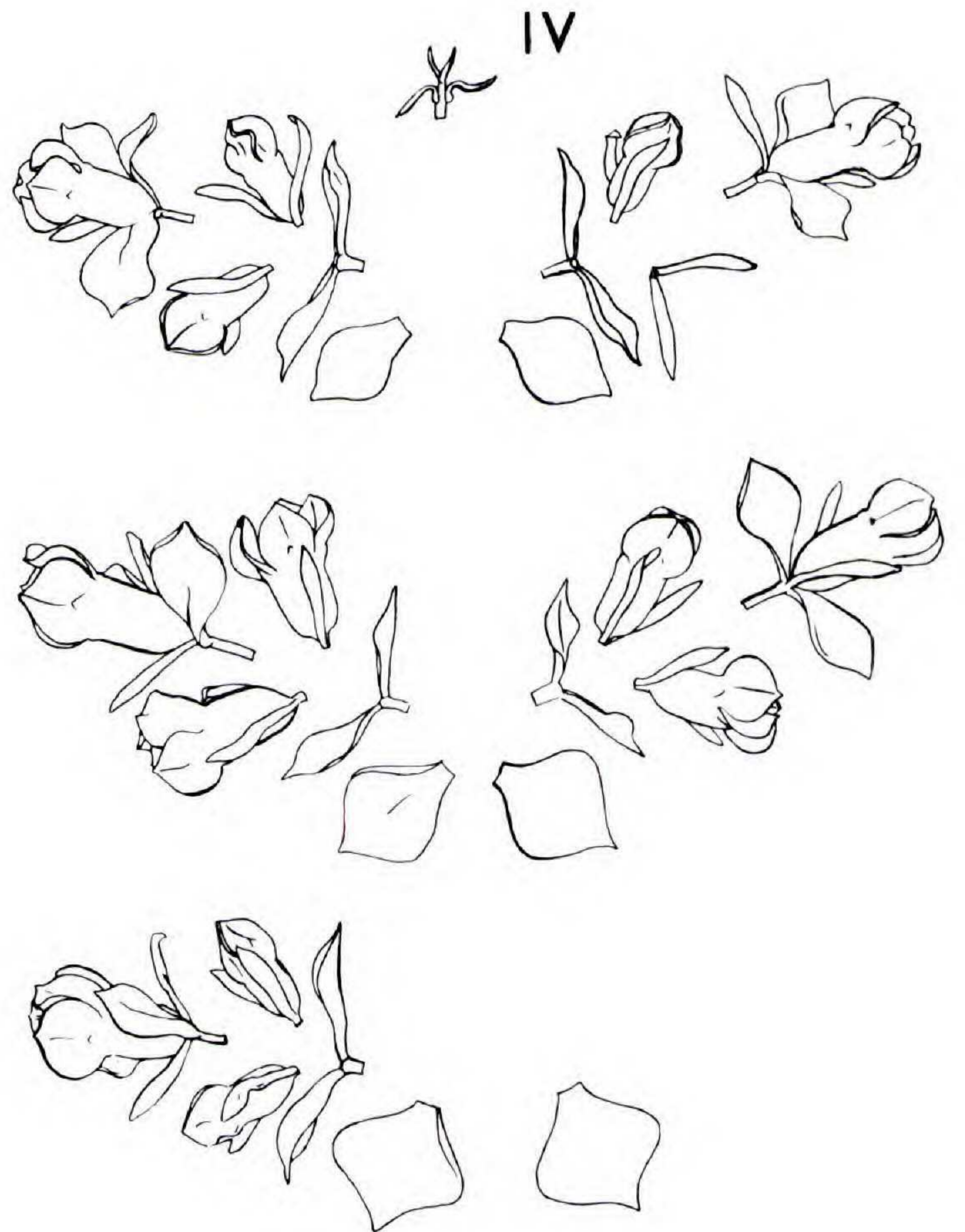
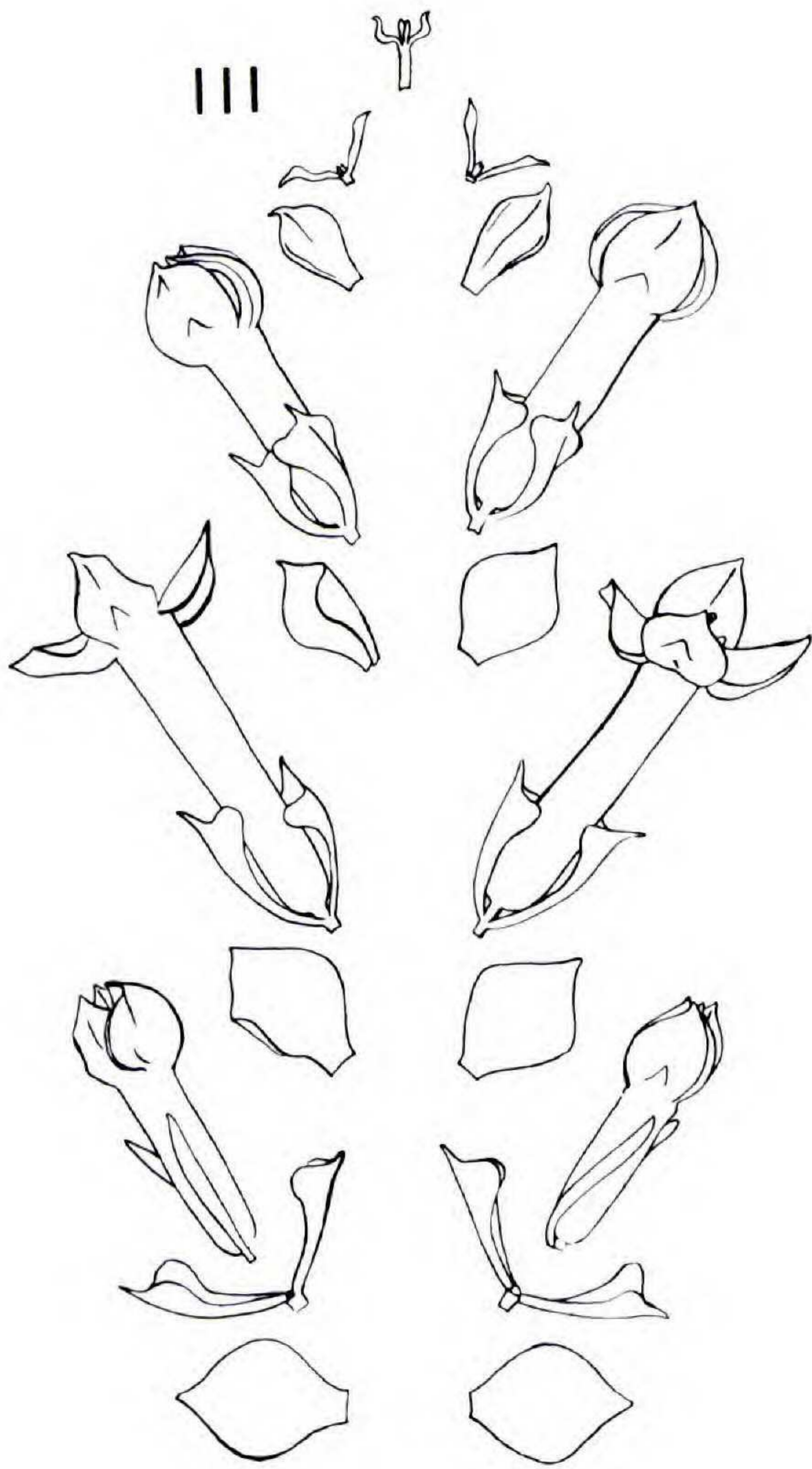


FIGURE 38. *Combretaceae*. *Conocarpus erecta*; diagram of a flowering branch.

erally with a terminal flower," whereas *P. mucronata* L. was reported as "with or without terminal flower," and *P. cneorum* Meerb. as "without or sometimes with a terminal flower, when well developed with 6-14 flowers." In our own investigations based on very restricted material only, we could only once find a terminal flower. An indeterminate (anauxotelic) inflorescence of *P. mucronata* is shown in Figure 42 II, a terminal flower in Figure 41 III. Dahlgren (1971: 8) stated that in general the "flowering sequence is acropetal, but when a terminal flower is present, this develops in head of the upper neighboring flowers." This feature is very typical for terminal flowers.

In all genera, innovation, i.e., the production of vegetative shoots continuing the ramification system and perhaps later producing



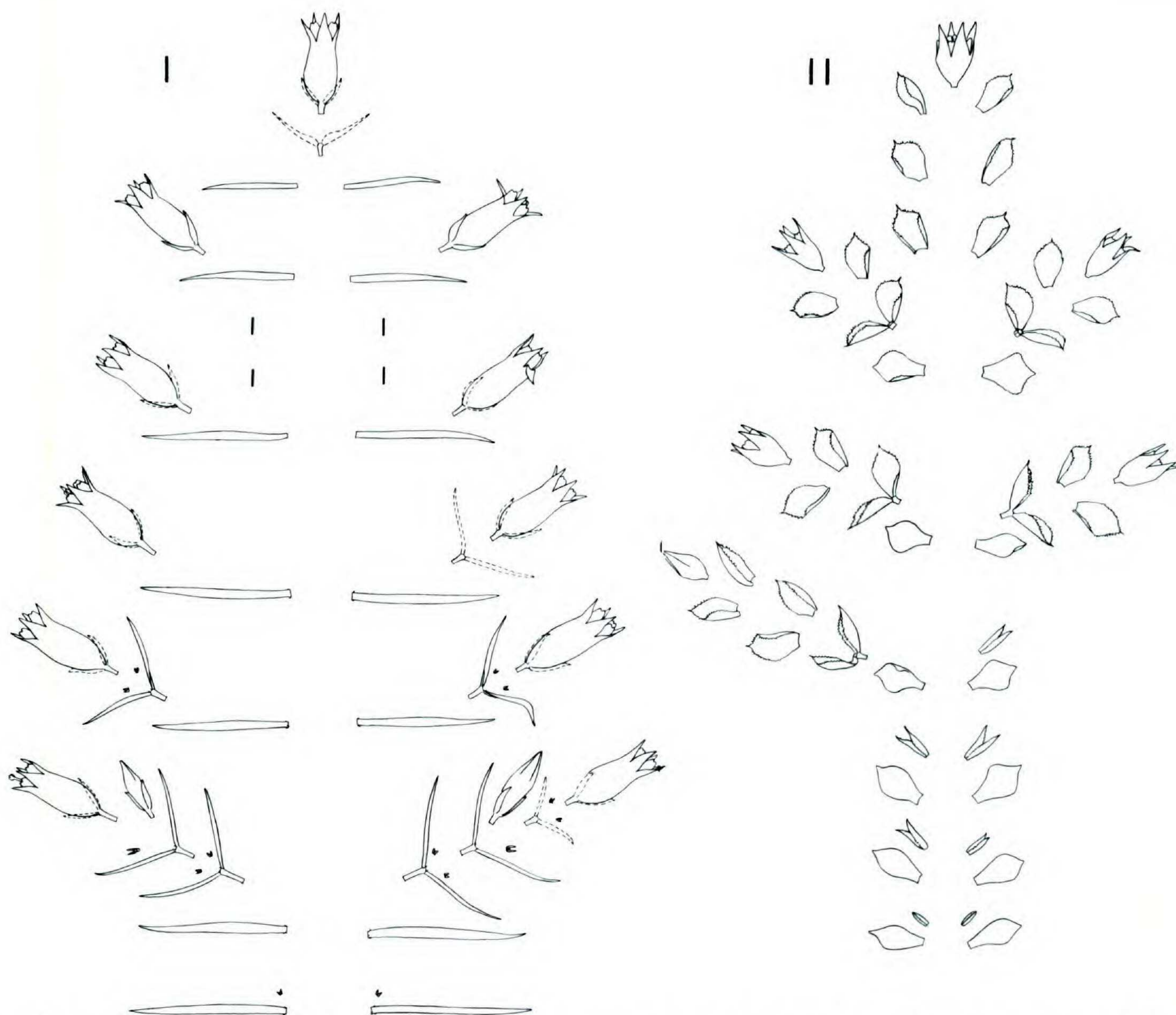


FIGURE 40. *Penaeaceae*. Semidiagrammatic representation of selected rich-flowered inflorescences.—I. *Stylapterus ericoides* (shed bracteoles with broken lines).—II. *S. fruticosus*. (All from Dahlgren.)

terminal inflorescences, takes place from the axils of foliage leaves somewhat below the flower-bearing zone.

Inasmuch as the spikelike inflorescences actually no longer develop a terminal flower, they could be interpreted as a botrytic polytelic main florescence. We hesitate, however, to classify them in this way, not only because terminal flowers are reported for some cases, but particularly because of the lack of paracladia terminating in co-florescences. If such paracladia could be found in well-developed inflorescences, this would prove that the strong

evolutionary tendency from the formation of monotelic inflorescences to the development of polytelic systems that appears independently in various branches of the family has really arrived at the polytelic stage. Without this proof we prefer to classify the indeterminate inflorescences as truncate monotelic systems.

A special case within the family is the inflorescence of *Endonema*. In both species, *E. lateriflora* (L. f.) Gilg and *E. retzioides* Sonder (Fig. 43 I), two or more single flowers are situated in the axils of leafy pherophylls

FIGURE 39. *Penaeaceae*. Semidiagrammatic representations of richly developed inflorescences.—I. *Saltera sarcocolla*. (South Africa. Cape Prov.: Forstmeier s.n.) —II. *Sonderothamnus petraeus*.—III. *Brachysiphon acutus*.—IV. *B. fucatus*. (II–IV from Dahlgren.)

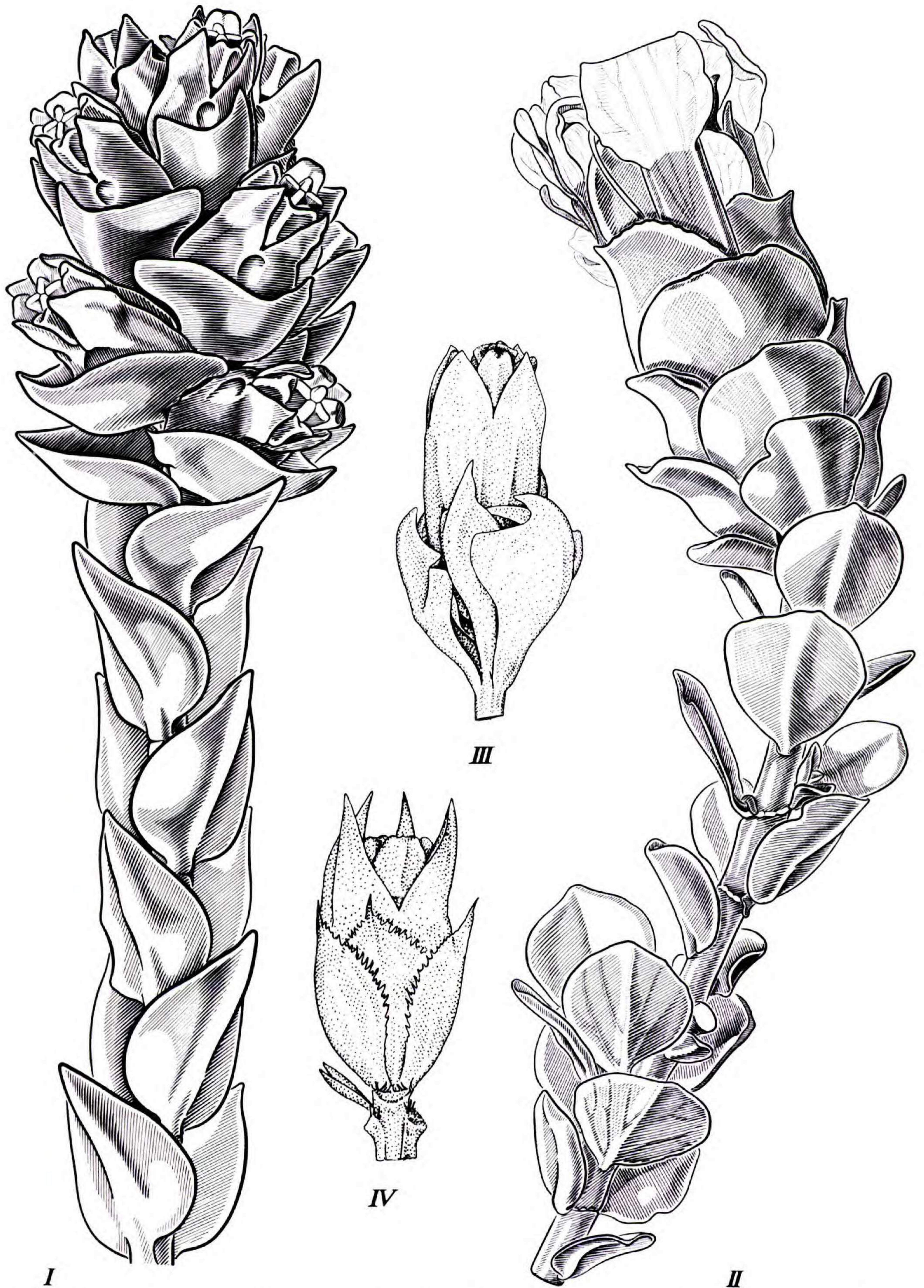


FIGURE 41. *Penaeaceae*. I, II. Flowering branches.—I. *Penaea mucronata*. (South Africa. Cape Prov.: near Elim, Weberling 7819.)—II. *Saltera sarcocolla*. (South Africa. Cape Prov.: Fernkloof, Hermanus, Weberling 7862a.)—III, IV. *Penaea mucronata* and *Stylapterus fruticosus*; terminal flowers subtended by three decussate pairs of bracteolate leaves or bracts. In IV the lowest pair is shed. (III, IV from Dahlgren.)

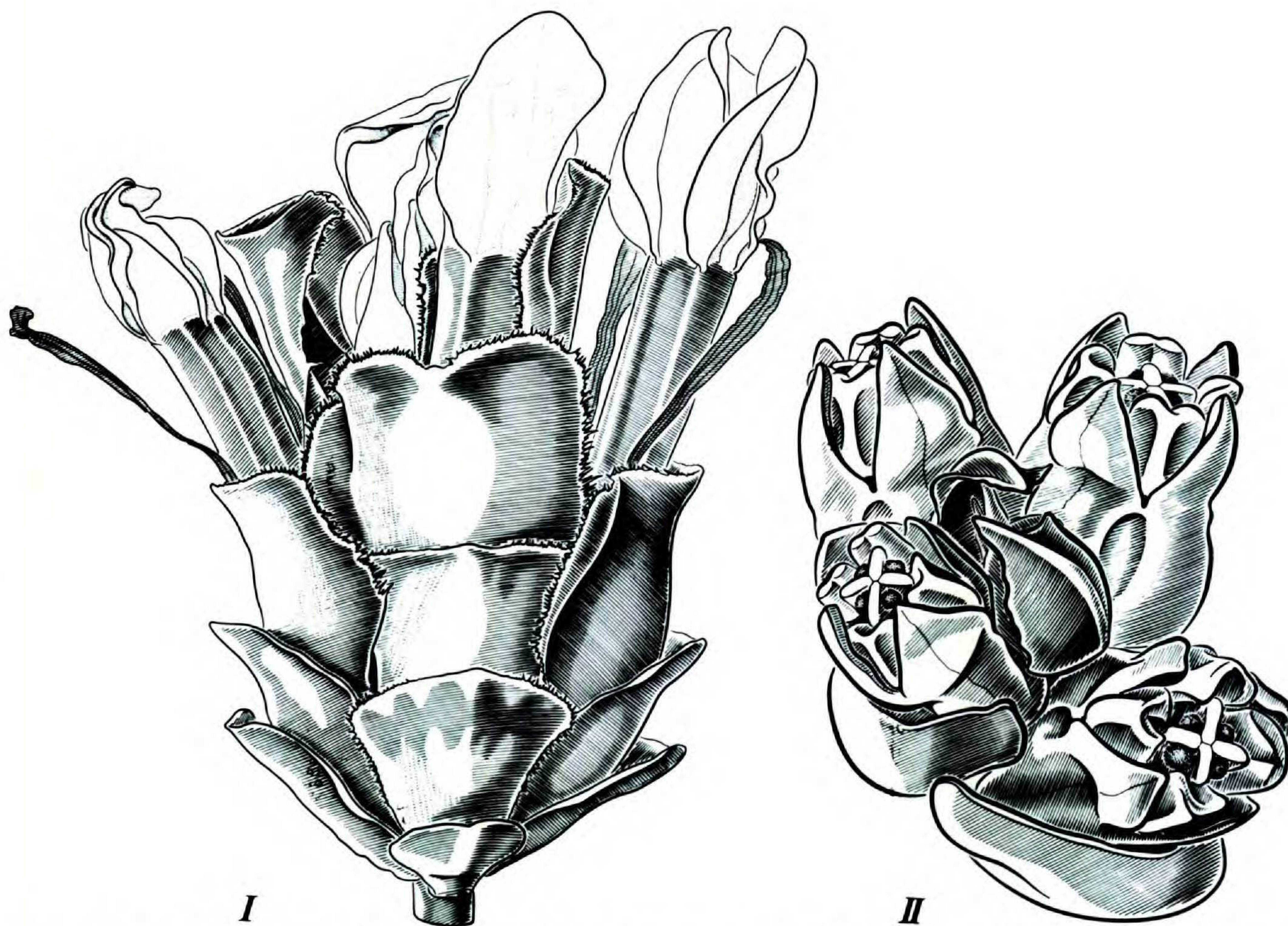


FIGURE 42. *Penaeaceae*.—I. *Saltera sarcocolla*; inflorescence. (South Africa. Cape Prov.: Weberling 7862a.) — II. *Penaea mucronata*; inflorescence apex ending in a sterile bud. (South Africa. Cape Prov.: Weberling 7819.)

on a young branch, which continues vegetative growth. Each of these lateral flowers bears two (*E. retzioides*) or three (*E. lateriflora*) pairs of bracts. Dahlgren (1967c) reported that suppressed buds are sometimes found in the axils of the lowest pair of “bracteoles.” Thus the whole branchlet in Figure 43 I may be explained as a proliferating monotelic inflorescence with highly reduced paracladia.

MELASTOMATACEAE

Variety of inflorescences in Melastomataceae corresponds to the size of the family but shows less diversity than Myrtaceae.

The inflorescences are monotelic throughout. Cases of complete transition to polytelic structures were not found. Even truncation seems to be rare. A single case noted by Troll (posthumous manuscript) is that of *Medinilla magnifica* Lindley, in which the inflorescence sometimes ceases development be-

fore the ultimate lateral cymes and the terminal flower of the distal thyrsic zone have completed their formation. Thus the whole end of the inflorescence atrophies (Fig. 64 III). Cremers (1983/1986) reported that the thyrses of *Desmoscelis villosa* (Aublet) Naudin remains indefinite. This, however, may only happen facultatively; in several plants investigated terminal flowers of the thyrsoids were well developed (Fig. 45). On the other hand, proliferation is not infrequent.

The basic form of ramification is a pleiothyrsoid terminating in a leafy shoot, as in *Miconia argentea* (Sw.) DC. (Fig. 44). Such bracteose or frondo-bracteose pleiothyrsoids, diplothyrsoids, or even monothyrsoids (haplothyrsoids) can be found in a terminal position in nearly all the 1,000 species of the genus *Miconia* as well as in many other ligneous genera such as *Conostegia*, most species of *Tococa*, and the large genera *Leandra* and *Clidemia*. Elongate conical thyrsoids or diplothyrsoids are also typical of many species

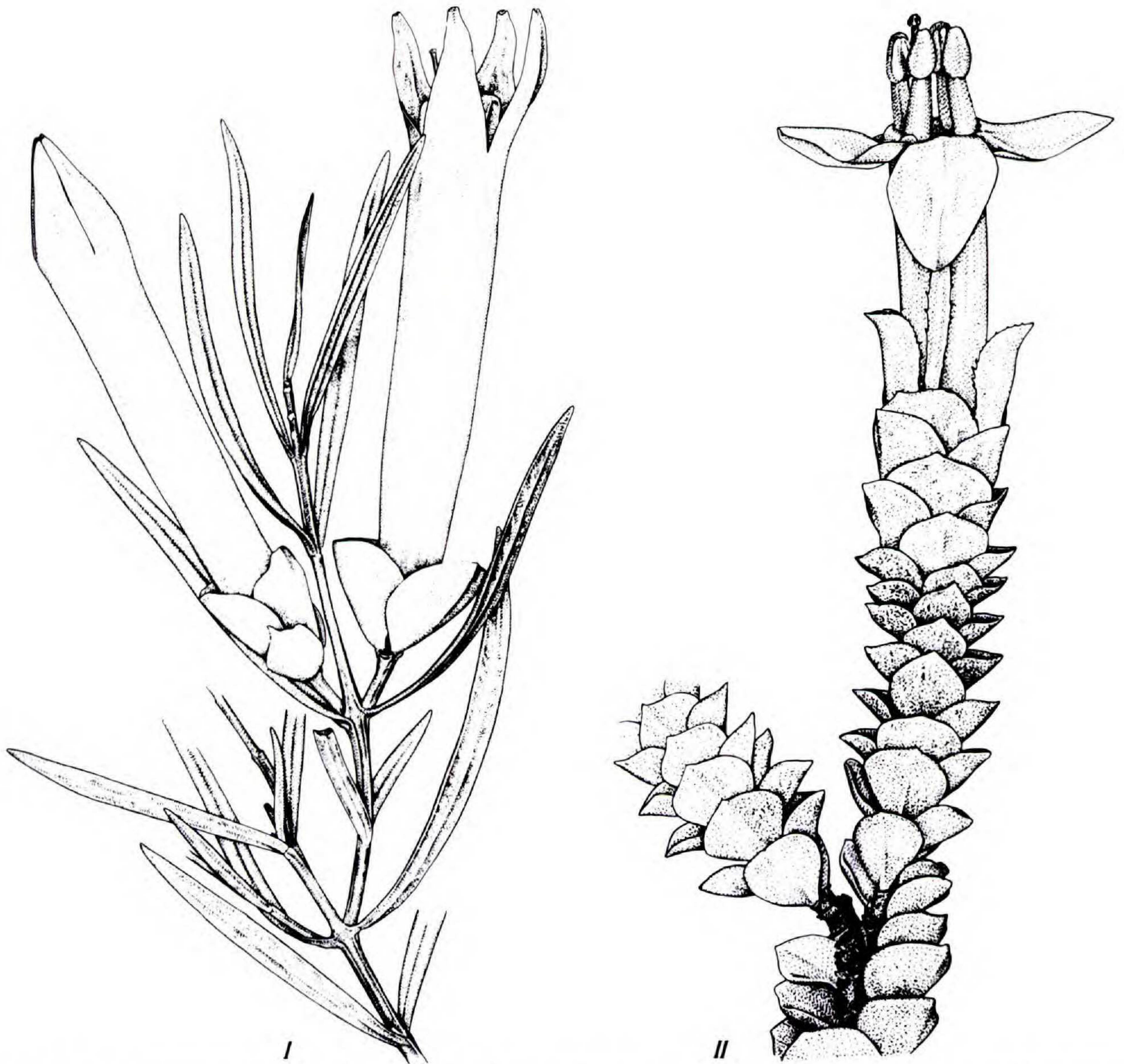


FIGURE 43. *Penaeaceae*.—I. *Endonema retzioides*; part of a branchlet with two uniflorous inflorescences.—II. *Saltera sarcocolla*; branchlet with terminal uniflorous inflorescence. (Both after Dahlgren, 1967c, 1968: I. Hohenacker s.n.; II. South Africa: S. Cape Peninsula, Dahlgren & Peterson 652.)

of *Tibouchina*. In some species of *Tibouchina* and of *Heterocentron*, the thyrsoids get a somewhat botrytic appearance since the hypopodia of the paracladia of first order are long compared with the other internodes ("thyrsus racemiformis"). Many examples have been analyzed and figured by Cremers (1983/1986), who published a thorough study on inflorescence structures of Guianese Melastomataceae. His investigations also include interesting studies on growth forms. While the manuscript of the present article was in press, W. S. Judd (1986) published the results of studies on variation in inflorescence position in *Miconieae*.

The cymose ramification of the partial inflorescences usually remains limited, and the mode of ramification is different. Eichler

(1878c: 483) observed a formation of a helicoid cyme (bostryx) by preferential ramification from the axils of the β -prophylls in *Tibouchina* (cited by Eichler as *Lasiandra*). A bostryx also is reported for *Centradenia floribunda* Planchon by Wydler (1878: 349), who supposed that ramification continued from the axils of the β -prophylls as in *Tibouchina*. Ziegler (1925: 410), however, observed a preferential ramification from the axils of the larger α -prophylls. The statement of Eichler (1878c: 483) that in the helicoids of *Centradenia* only the fertile prophylls are developed proved to be wrong (Troll, posthumous manuscript). Krasser (1893) reported helicoid cymes for *Miconia secundiflora* Cogn. Simple or double helicoids also occur in *M. hookeriana* Triana (Fig. 46 I) and *Fordiophyton*.



FIGURE 44. *Melastomataceae*. *Miconia argentea*; monotelic pleiothyrsoid inflorescence. (El Salvador: Weberling 2024.)

The formation of scorpioid cymes (cincinni) by preference of the ramification from the axils of the α -prophylls was reported by Eichler (1878c: 483) for *Salpinga* and *Clidemia*. Scorpioid ramification of the cymose partial inflorescences is also known for *Rhynchanthera* (Wydler, 1851a: 370), the Bertolonieae and Sonerileae (see Krasser, 1893, and p. 278), *Arthrostema*, *Centradenia inaequalateralis* (Schldl. & Cham.) G. Don (see p. 282), *Amphiblemma cymosum* (Schrader & Wendl.) Naudin (see p. 272), *Appendicularia thymifolia* (Bonpl.) DC., and *Aciotis acuminifolia* (DC.) Triana, *A. acutiflora* (Martius) Triana, *A. longifolia* Triana, and others.

The cymose paracladia in the mono-thyrse inflorescence of *Miconia hookeriana* Triana are simple helicoid cymes in the distal part, and double helicoid cymes in the proximal part (Fig. 46 I). The inflorescence, which has only caducuous bracts, is preceded by several pairs of foliage leaves bearing vegetative buds in their axils. From the axils of older leaves sylleptic branches with several

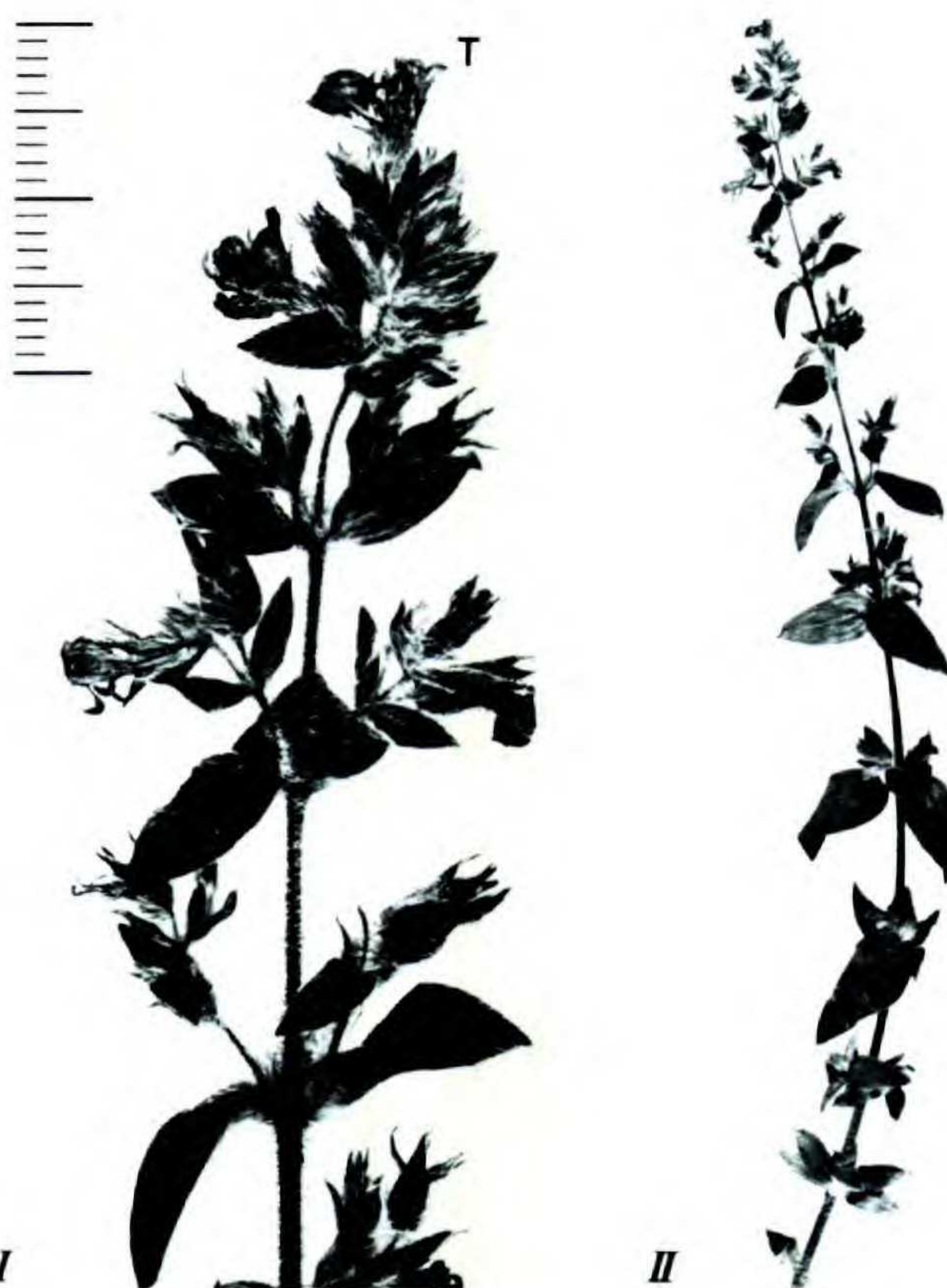


FIGURE 45. *Melastomataceae*. *Desmoscelis villosa*. (N. Brazil: Ph. v. Luetzelburg 22181 (M).) —I. Distal part of II. T, terminal flower.

foliaceous leaves and a terminal thyrseoid can develop (Fig. 46 II).

In most of the ligneous *Melastomataceae*, the axillary buds of the leaf pairs preceding the terminal inflorescence develop innovation shoots some time after anthesis, as is shown here for *Miconia guatemalensis* Cogn. (Fig. 47 II). The order of precedence in this development can be indicated already by the size of the buds (Fig. 47 I).

On the other hand, there are ligneous members of the family with proliferating inflorescences. A favorable disposition for proliferation seems to be given with the occurrence of leafy pherophylls, as in *Huilea macrocarpa* Uribe (Fig. 47 III). After the production of long-peduncled axillary thyrseoids or cymes the apex of the inflorescence axis returns to vegetative growth, producing axillary buds that develop vegetative branches instead of flower-bearing paracladia (Mora Osejo, 1966). Among the numerous species of *Clidemia*, which mostly have terminal bracteose thyrseoid or diplothyrsoid inflorescences, there is *C. rubra* (Aublet) Martius

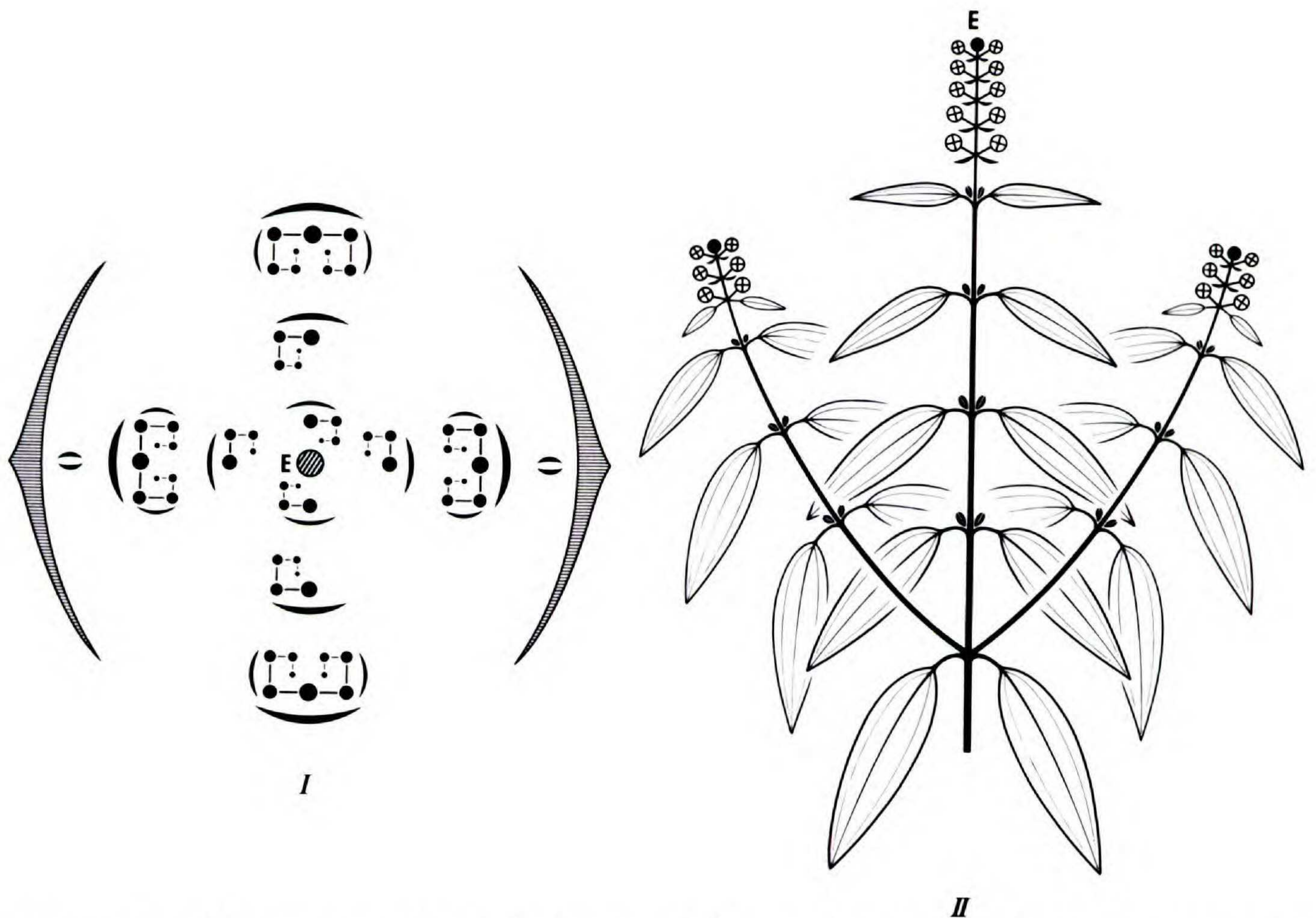


FIGURE 46. *Melastomataceae*. *Miconia hookeriana*.—I. Horizontal projection of the ramification of a thyrsoid.—II. Vertical projection of a flowering branch system. (From Troll.)

with leafy proliferating inflorescences (Fig. 48 I). In contrast to *Huilea macrocarpa*, however, the paracladia in *C. rubra* are reduced to sessile densely flowered cymes.

Proliferation also can be observed within the genus *Comolia*, which also comprises some herbaceous species with proliferating inflorescences (Cremers, 1983/1986). Proliferating inflorescences are characteristic of many or all species of many additional genera, including *Amplectrum* (*homoeandrum* Stapf), *Blastus*, *Bellucia*, *Cambessedesia*, *Ernestia*, *Maieta*, *Marumia*, *Mecranium*, *Meriania*, *Microlicia* (*M. pseudo-scoparia* Cogn.), *Micropophysca*, *Myriaspora* (*M. egensis* DC.), *Myrmidone*, *Ochthocharis*, *Opisthocentra*, *Ossaea*, *Plethiandra*, *Tococa*, *Trembleya*, and others. In *Acanthella*, the paracladia of the proliferating inflorescence are reduced to single flowers; the same applies to species of *Blakea* (*B. spruceana* Cogn., see fig. 80 in Krasser, 1893), *Kibessia*, *Pyxidanthus*, and *Topobea*. *Topobea* and *Blakea* are placed in

the Blakeae, which is characterized by the flowers bearing an involucre of two or more pairs of bracts. This may be interpreted as the remnant of a formerly richer ramification. In addition, in many species of *Blakea* and *Topobea*, we found one to three accessory single flowers below the original one.

Delayed anthesis of the paracladia of proliferating inflorescences in such ligneous plants results in a more or less pronounced cauliflory. Thus in contrast to *Clidemia rubra*, which was mentioned above for its proliferating inflorescences, *C. septuplinervia* Cogn. is cauliflorous (Cremers, 1983/1986). The same applies to many Memecyloideae. Nearly all species of this subfamily are characterized by auxotelic (or sometimes anauxotelic) inflorescences or by more or less cauliflorous partial inflorescences. Transitional forms may be found even in the same plant. Only in *Memecylon cumingianum* Presl we found axillary and terminal thyrsoids. The latter, however, were terminating an older ligneous stem

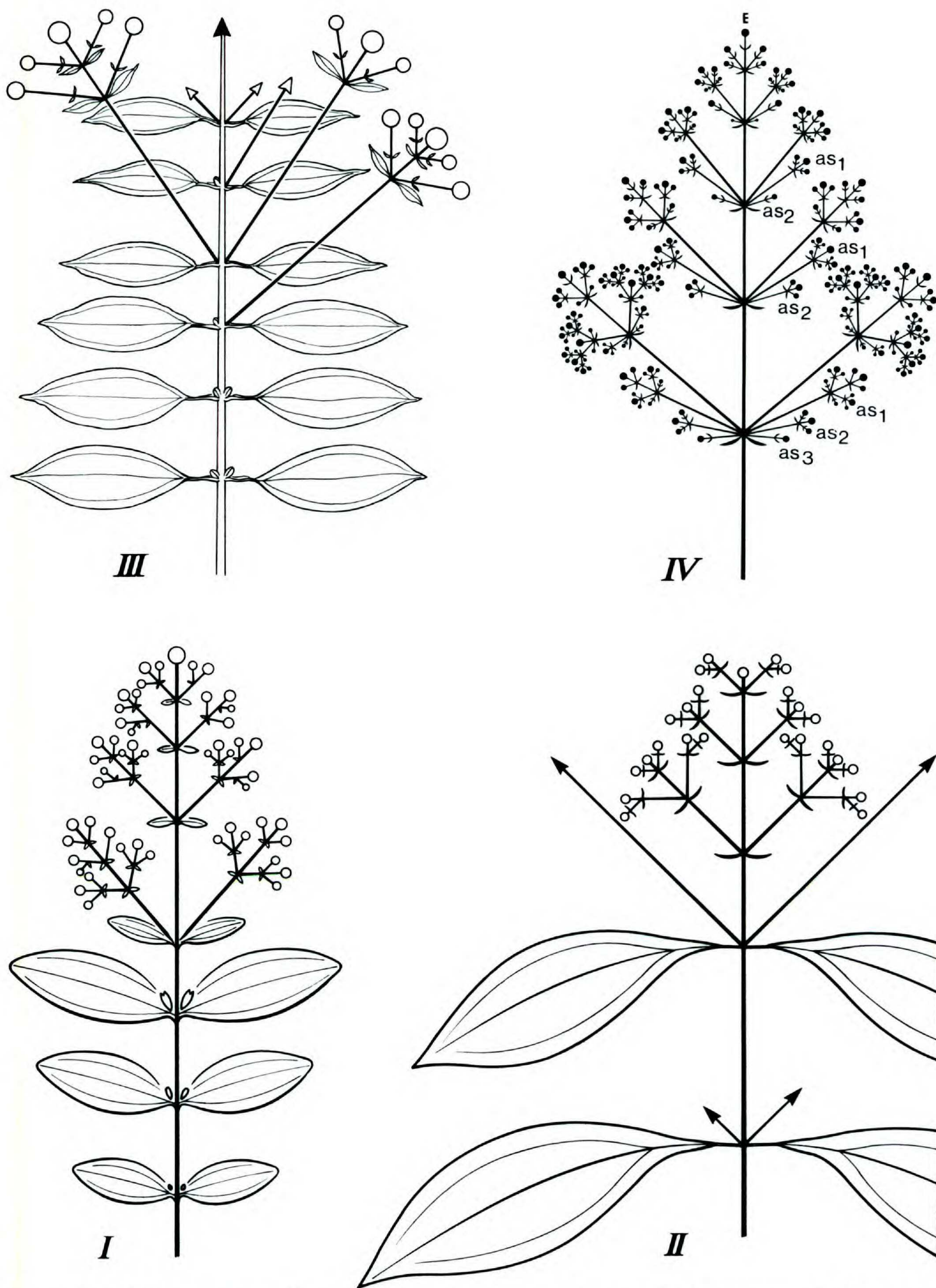


FIGURE 47. *Melastomataceae*. Vertical diagrams of flowering shoots and inflorescences.—I. *Miconia squamulosa* (from Mora).—II. *M. guatemalensis*. (El Salvador; Weberling 2299.)—III. *Huilea macrocarpa*; with a proliferating inflorescence axis (from Mora.)—IV. *Tococa symphyandra*; synflorescence with accessory flower-bearing branches of first to third order (as_1 – as_3). (All from Troll.)



FIGURE 48. *Melastomataceae*.—I. *Clidemia rubra*; proliferating flowering shoot. (El Salvador: La Palma, Weberling 732.)—II. *Tococa spadiciflora*; spadixlike inflorescence (from Troll).—III. *Henriettella macfadyenii*; cauliflorous branch (from Troll.)

that was still bearing its foliage leaves. Cauliflory is also well known for the genera *Loreya*, *Henriettea*, *Henriettella* (e.g., *H. macfadyenii* (Triana) Alain (Fig. 48 III), and *H. glazioviana* Cogn., see fig. 79B in Krasser, 1893), *Bellucia* (e.g., *B. imperialis* Sald. & Cogn.), and *Myriaspora*. All of these genera belong to the Miconieae, which also includes *Clidemia*.

The contours and forms of terminal inflorescences can be modified by different features. Thus the conical thyrsoid, as mentioned already for *Conostegia* or *Miconia* (Figs. 44, 47 I), can be transformed into a corymboid by more or less effective suppression of the internodal growth of the inflorescence axis, combined with pronounced basitonic development of the paracladia and especially prolongation of their hypopodia. Two shrubs,

Fordiophyton fordii (Oliv.) Krasser and *Dichaetanthera corymbosa* (Cogn.) Jacques-Félix (see Krasser, 1893: 156), may be mentioned as examples.

In *Amphiblemma cymosum* (Schrad. & Wendl.) Naudin (Fig. 49), a corymboid of pleiochasial structure is formed. The internodes in the distal part of the inflorescence axis, with the exception of the final internode, remain very short. As a result the insertions of the paracladia are crowded together (Fig. 49 I). The arrangement of these paracladia is not decussate as might be expected, but alternate, since phyllotaxis changes above the uppermost pair of foliaceous leaves, which is usually somewhat smaller. The bracteose perophylls of the paracladia are shifted on their axillary paracladia by recaulescence. Usually there are five paracladia (maximum

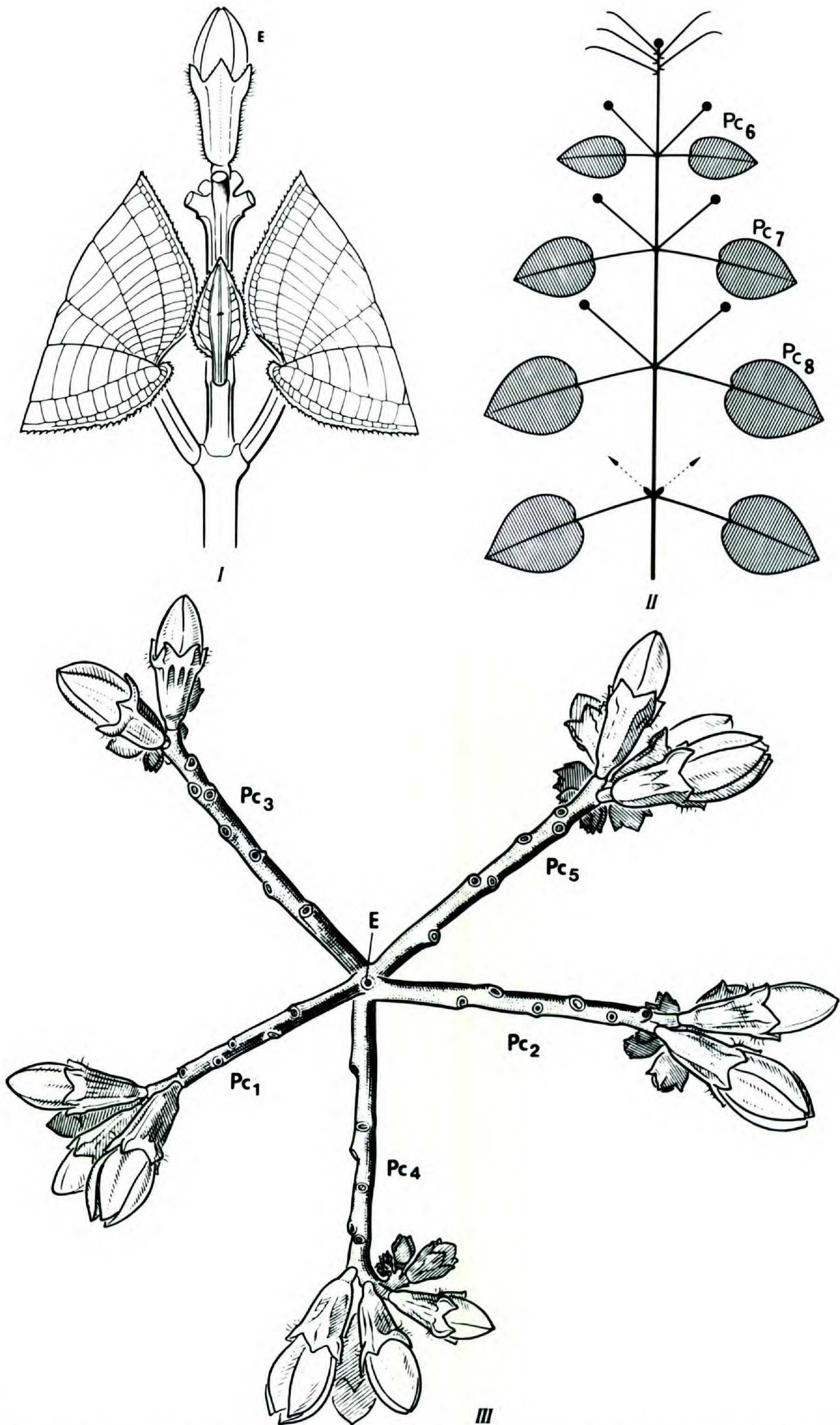


FIGURE 49. *Melastomataceae*. *Amphiblemma cymosum*.—I. Inflorescence apex, the paracladia have been cut off.—II. Vertical projection at the beginning of anthesis of a flowering shoot.—III. Pleiochasial corymboid at the end of anthesis from above. Pc_1 – Pc_5 , paracladia of first to fifth order; E, terminal flower. (All from Troll.)

eight) forming helicoid cymes. If there are more than five paracladia, the lower ones can form "paired" or "double helicoids," because in these more vigorous paracladia both first-order prophylls are fertile. Since the paracladia elongate considerably by the formation of many flowers, the position of the terminal flower finally is at the deepest point of the whole pleiochasium (Fig. 49 III). In older and vigorous plants more paracladia, mostly double-helicoid, can develop from the axils of the foliaceous leaf pairs in the lower part of the stem (Fig. 49 II, pc_6 – pc_8).

The monotelic (pleio-)thyrsoid as the basic form of inflorescences in Melastomataceae can also be modified by reduction of 1) the ramification of the paracladia and 2) the number of paracladia.

1) Reduction of cymose ramification of the paracladia ultimately results in the formation of dibotryoids, as shown for *Leandra sylvatica* Cogn. or *Miconia sarmentosa* Cogn. by Cremers (1983/1986, figs. 25/3, 27/2; see also *Tibouchina frigidula* (DC.) Cogn., fig. 30/2), or in the formation of simple botryoids. A transitional stage on the way to formation of botryoids is exemplified by *Tococa guianensis* Aublet (Fig. 50 II). Compared with other elongate thyrsoids like that of *Tococa formicaria* Martius (Fig. 50 III) or *Allomorpha magnifica* Guill. (Fig. 50 I), its ramification appears to be much reduced, although the proximal paracladia are still three-flowered. If these paracladia are reduced to uniflorous elements, the inflorescence forms a simple botryoid, as occurs facultatively in *Tibouchina canescens* (D. Don) Cogn. (Cremers, 1983/1986, fig. 30/5), *Clidemia capitellata* (Bonpl.) DC. (Fig. 51 III), and *C. minutiflora* (Triana) Cogn. (Cremers, 1983/1986, fig. 32/7), or generally in *Adelobotrys spruceana* Cogn. (Cremers, 1983/1986, fig. 19/9) or *Castratella piloselloides* (Bonpl.) Naudin (Cremers, 1983/1986, fig. 19/9).

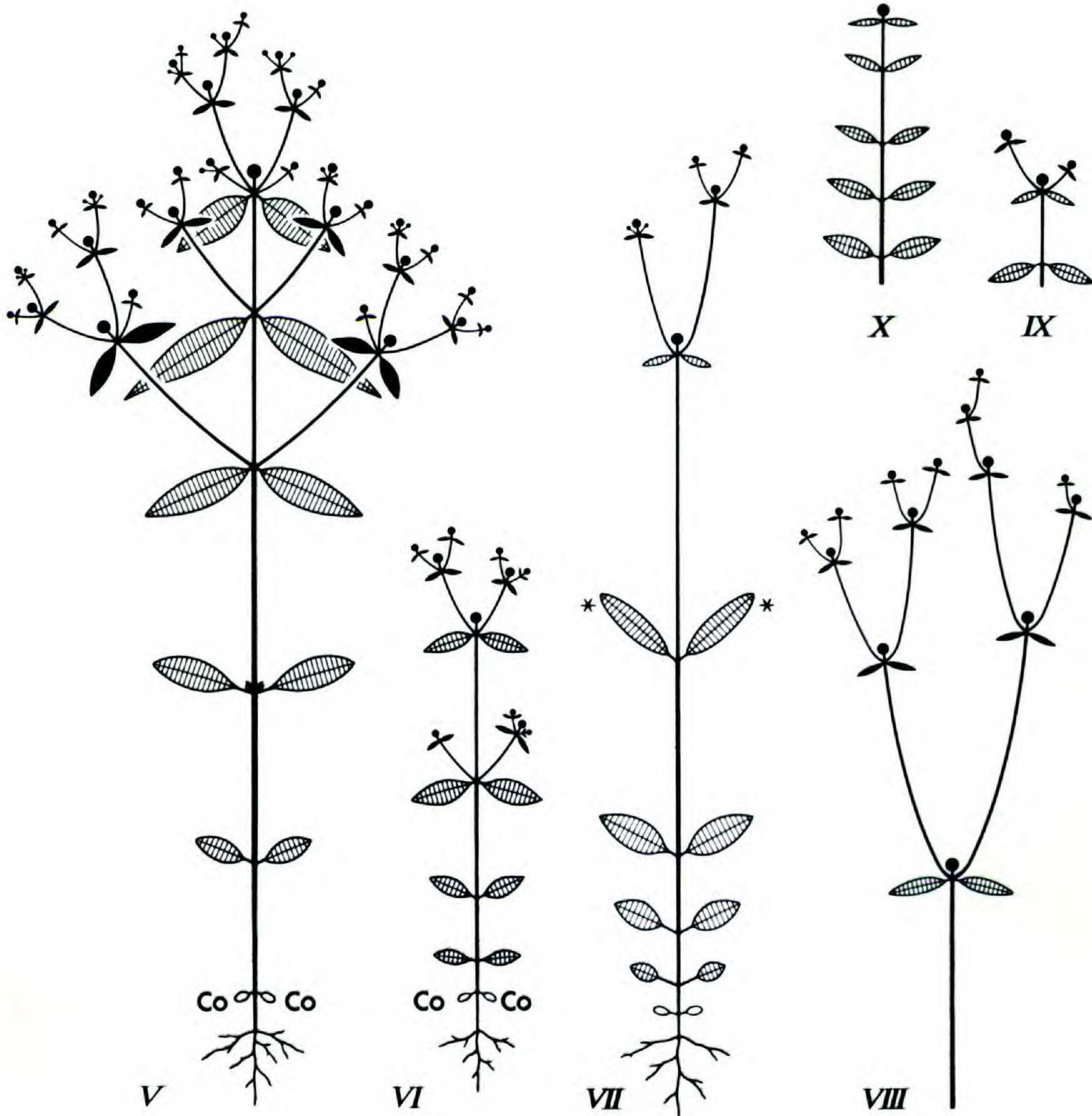
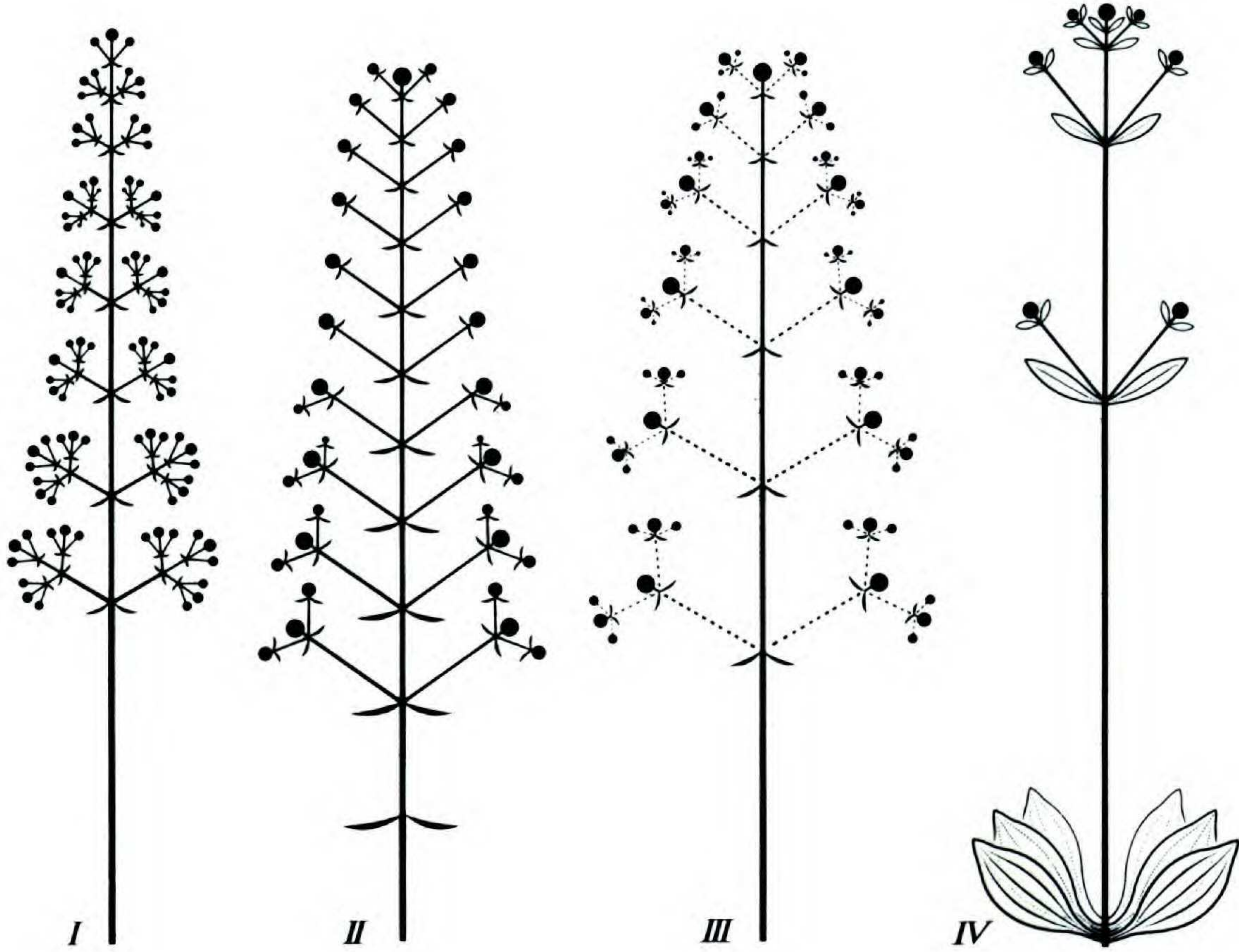
In another way the dense spikelike or nearly spadix-formed inflorescence of *Tococa spadiciflora* Triana (Fig. 48 II) can be derived from an elongate monothyrsoid: as indicated in Figure 50 III, the hypopodia of first and second orders (dotted lines) remain undeveloped. If this is combined with a shortening of the main axis, a capitulate inflorescence like that of *T. capitata* Cogn. (= *Sagraea capitata* Triana) results. According to Troll (posthumous manuscript), the inflorescence apex of *T. spadiciflora* probably remains indefinite.

If in contrast to the previous examples all internodes of the inflorescence are prolonged, a loosely branched thyrsoid results, as in *Nepsera aquatica* (Aublet) Naudin (Fig. 57 I).

As already mentioned for ligneous members of the family, foliaceous proliferating botrytic inflorescences are not rare (see also *Tibouchina axillaris* Cogn., Fig. 51 I). *Comolia purpurea* Miq. (Cremers, 1983/1986, fig. 22/1) and *Tibouchina petroniana* Cogn. (Cremers, 1983/1986, fig. 30/8), with its diplobotrytic inflorescences, are herbaceous examples.

2) This reduction of cymose ramification of the paracladia resulting in the formation of botryoids can be combined with diminution of the number of paracladia. Thus the botryoids of *Castratella piloselloides* mentioned above (Fig. 50 IV) bear two or three pairs of paracladia only. Reduction can go further, as in *Clidemia involucrata* DC., with sometimes only two uniflorous paracladia below the terminal flower (Cremers, 1983/1986, fig. 21/11). Ultimately a solitary terminal flower remains, as in the fruticose *Tibouchina sellowiana* (Cham.) Cogn. and *T. petroniana* Cogn. (Fig. 51 II; Cremers, 1983/1986, figs. 30/6, 7). Cogniaux (1888: 598) described the flowering system of the latter as "floribus ad apices ramulorum solitariis; bracteis saepius 6." Indeed, the main axis and a series of

FIGURE 50. Melastomataceae. Vertical diagrams of inflorescences and flowering plants.—I. *Allomorpha magnifica*.—II. *Tococa guianensis*.—III. *T. formicaria*; the hypopodia (dotted lines) remain completely undeveloped in *T. spadiciflora*.—IV. *Castratella piloselloides*. V–X. Rich- and poor-flowered plants of *Pterolepis trichotoma* (V, VI); *P. repanda* (VII, VIII); and *P. pauciflora* (IX, X). (All from Troll.)



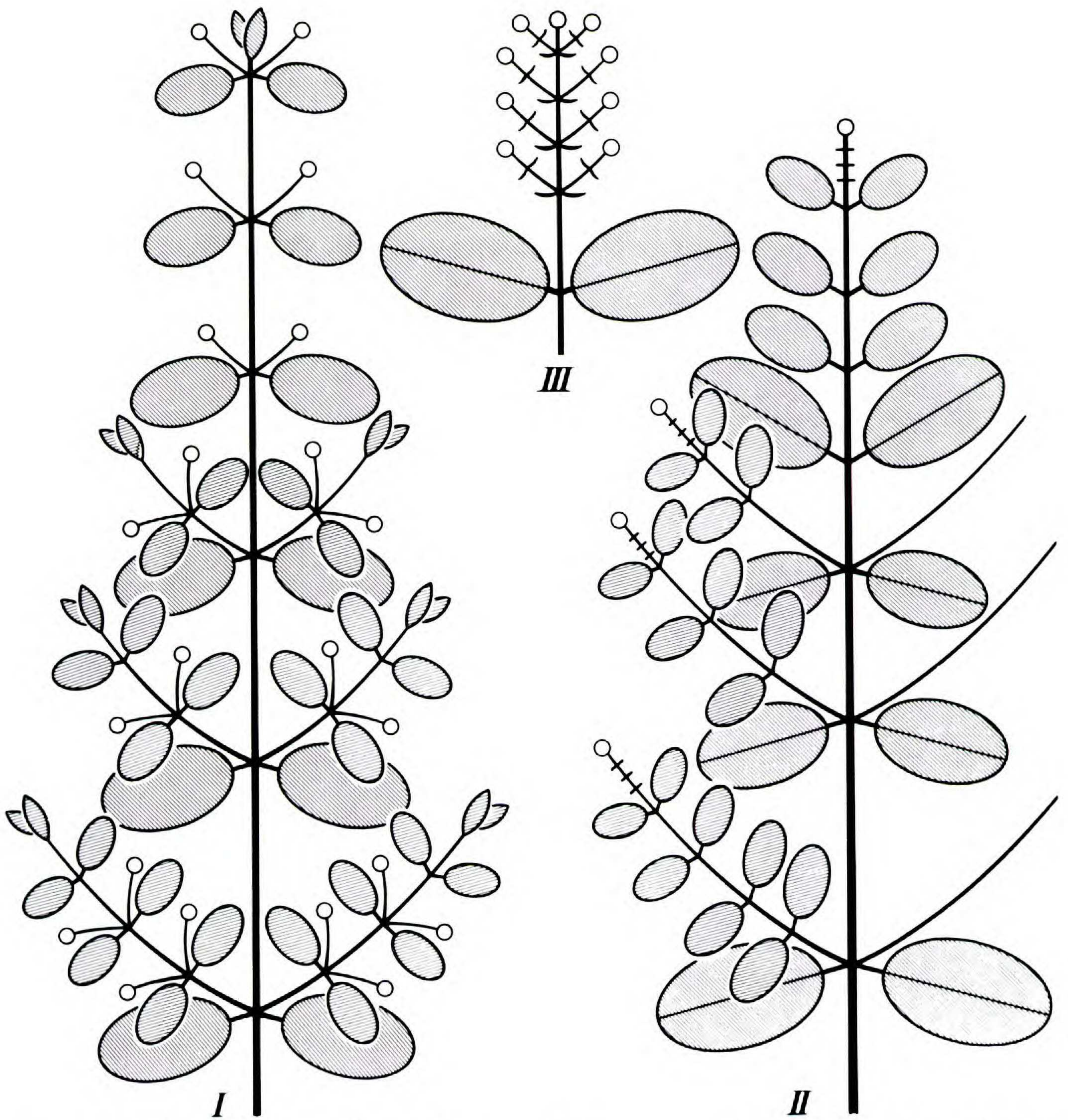


FIGURE 51. *Melastomataceae*. Vertical diagrams of inflorescences.—I. *Tibouchina axillaris*.—II. *T. petroniana*.—III. *Clidemia capitellata*. (I, II diagrams according to Martius, *Flora Brazil*. XIV/3, pl. 92, XIV/4, pl. 128; III after Cremers, modified.)

foliaceous paracladia originating from the axils of foliaceous leaf pairs in the proximal part of the main axis bear a single terminal flower only. Each of these flowers is preceded by three pairs of sterile bracts—a remnant of the thyrsoid ramification system.

In the prevalently herbaceous genus *Salpinga* were found two-flowered inflorescences in *S. pusillum* (Gleason) Wurd. (= *Macrocentrum pusillum*) and uniflorous inflorescences in *S. glandulosum* (Gleason) Wurd., whereas within the related genus *Macrocen-*

trum, *M. cristatum* (L. C. Rich.) Triana apparently has cymoids with scorpioid paracladia (Krasser, 1893, fig. 75C); the same applies to *M. latifolium* Wurd. (Cremers, 1983/1986: 69). According to Cremers (1983/1986, fig. 25/5, 5'), *M. vestitum* Sandw. normally develops the terminal flower only, but in some exceptional cases this can be accompanied by two lateral flowers.

In such cases uniflory is obviously facultative. This especially applies to individuals of herbaceous annual species grown under

unfavorable conditions. In such plants the ramification is more or less reduced, sometimes with the result that only the terminal flower is developed. According to Troll (posthumous manuscript), examples can be found within the genus *Pterolepis*, which is closely related to *Tibouchina*. Figure 50 shows vigorous (V) and reduced (VI) plants of *P. trichotoma* Cogn., which differ in the number and the vigor of their cymose paracladia. In Figure 50 V the lowest pair of paracladia has the longest hypopodia of first and second orders and is the most copiously branched. The uppermost pair of paracladia, however, is also vigorous and bears more flowers than the preceding one. This indicates a certain tendency of an acrotonic support of ramification. Therefore it is not surprising that in the reduced plant (Fig. 50 VI) the distal pair of paracladia is the only one fully developed. In *P. repanda* (DC.) Triana (Fig. 50 VII, VIII) the acrotonic support of ramification becomes so effective that only the distal pair of paracladia is developed and a more (VIII) or less (VII) copiously branched cymoid is formed. In *P. pauciflora* (Naud.) Triana pauperization of the inflorescence finally progresses to the formation of a three-flowered (Fig. 50 IX) or uniflorous (X) inflorescence. Some other examples have been given by Cremers (1983/1986), who analyzed species of *Acisanthera* and *Appendicularia* and found uniflorous individuals in *Acisanthera bivalvis* (Aublet) Cogn. (Cremers, 1983/1986, fig. 18/8); a similar diversity of inflorescence forms occurs in *Appendicularia thymifolia* (Bonpl.) DC. Altogether the inflorescences of the mostly or exclusively annual species of *Acisanthera*, *Appendicularia*, *Aciotis* (e.g., *A. amazonica*, *A. aequilateralis*, *A. dichotoma* Cogn.), and probably also *Pterogastra* are very variable: plants with extremely acrotonic ramification forming "dichotomic" inflorescences (cymoids) can be found beside plants with extremely reduced, sometimes even uniflorous inflorescences. The herbaceous *Catacoryne linnaeoides* Hook. f. probably also can develop uniflorous inflorescences.

Obligatorily uniflorous inflorescences are known for some fruticose taxa, especially the

genus *Chaetostoma* and some species of the genera *Marcetia*, *Lavoisiera*, and *Microlicia*.

A flower-bearing shoot system of *Marcetia sertularia* DC. (Fig. 52 III) shows the branches more vigorously developed in the distal zone, i.e., an acrotonic ramification system. Most of the densely foliate branches as well as their relative main axes end in a terminal flower (Fig. 52 II). Lateral flowers or even vestiges of lateral flowers inserted below the terminal flowers cannot be found, in contradistinction to some other species of the genus. The whole system, however, cannot be regarded as an entire inflorescence but must be interpreted as a ramification system comprising numerous uniflorous inflorescences.

Accessory buds or branches are very common within the family (see also Wagner, 1907). They form single flowers or dyads in the inflorescence of *Pterolepis trichotoma* (Rottb.) Cogn. (Fig. 50 V) and occur in the leaf axils of the main axis as well as of the paracladia and can even form triadic or many-flowered cymes, as in *Adelobotrys ciliata* (Naudin) Triana, *A. permixta* Wurd., *Leandra polyadena* Ule, and *L. rufescens* (DC.) Cogn. (Cremers, 1983/1986, figs. 19/2, 6, 24/1, 4), or even thyrsoid flowering systems, as in *Miconia kappleri* Naudin and *M. tillettii* Wurd. (Cremers, 1983/1986, figs. 26/1, 2). If there are two or more buds, they are always arranged in a phylloscopic sequence, as in *Topobea guianensis* Aublet (Cremers, 1983/1986, fig. 31/6) or *Creochiton* Bl. (see Wagner, 1907). Sometimes differentiation between the buds of the same axillary series can take place. In *Ernestia confertiflora* Wurd. the upper of two buds develops into a vegetative branch and the lower forms a flowering system, whereas in *Maieta guianensis* Aublet the reverse situation occurs (see Cremers, 1983/1986, figs. 23/5, 25/6). Troll (posthumous manuscript) found in an inflorescence of *Tococa symphyandra* (Triana) Cogn. that 92 of a total 220 flowers belonged to accessory branches (Fig. 47 IV).

The formation of cymoids has been mentioned already in the context of the reduction

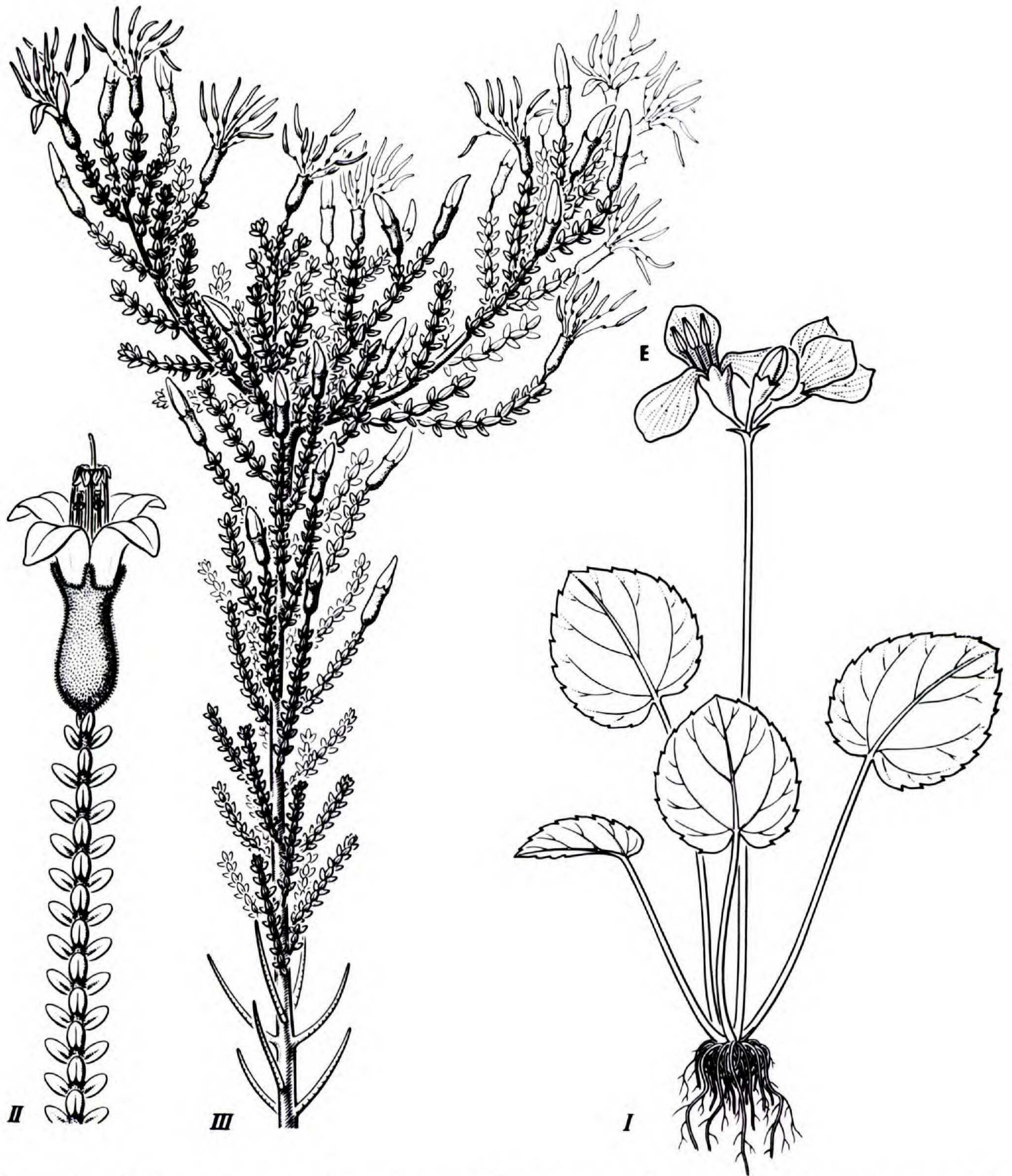


FIGURE 52. *Melastomataceae*.—I. *Sonerila rotundifolia*; flowering plant (after Beddome). E, terminal flower. II, III. *Marcetia sertularia*.—II. Single branch with terminal flower (after De Candolle).—III. Flowering branching system.

of inflorescences in reduced individuals of *Pterolepis* species (p. 277). Cymoids occur especially within the mostly herbaceous *Sonerileae* and *Bertolonieae*. Only a few examples are needed here.

In *Calvoa sessiliflora* Cogn. (*Sonerileae*) the cymoids are very conspicuous, especially in fruiting plants (Fig. 53 II). In this plant the leaves of the main axis are already lost. The foliation of the main stem is leafy and

only the distal pair of leaves is bracteose (Fig. 54 I). These bracts are inconspicuous and by recaulescence united with their axillary branches, the uppermost paracladia, which form simple scorpioids. Between these two scorpioids the main axis ends with the terminal flower that is sessile because the final internode remains undeveloped. The same applies to the flowers of the scorpioid paracladia. The internode preceding the insertion of the



FIGURE 53. *Melastomataceae*.—I. *Sonerila margaritacea*.—II. *Calvoa sessiliflora*; flowering plant. (From Troll.)

scorpioid paracladia is very thin in proportion to the other internodes of the main stem. The same difference appears between the scorpioids and the preceding paracladia, which in thickness attain about double the size. These paracladia, which originate from the axils of foliage leaves, repeat the architecture of the main stem: they end in a cymoid and their foliation is leafy, with the exception of the pherophylls bearing the scorpioids. However, there is one important difference: the leaf pairs, especially that in the median position are anisophyllous, and the leaf pointing outwards by far exceeds the size and differentiation of its partner (Fig. 54 II). The trans-

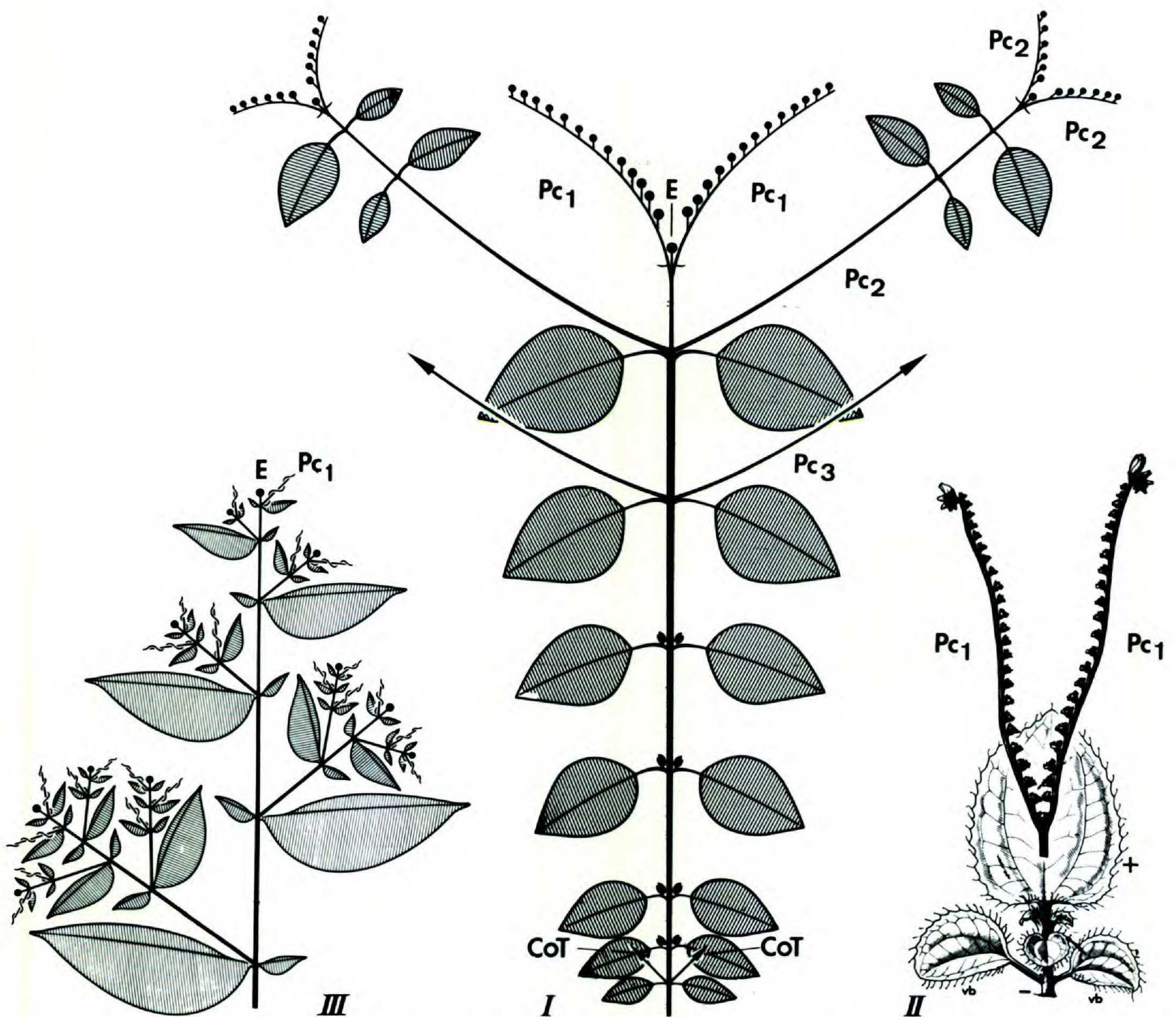


FIGURE 54. *Melastomataceae*. I, II. *Calvoa sessiliflora*.—I. Vertical diagram of a flowering individual; E, terminal flower; CoT, cotyledonary branches.—II. Paracladium (Pc_2 from I), view from the ventral (upper) side; vb, prophylls; +, the larger leaf of the anisophyllous second leaf pair.—III. *Centradenia grandifolia*; analytical vertical diagram of a flowering branch. (II, III from Troll.)

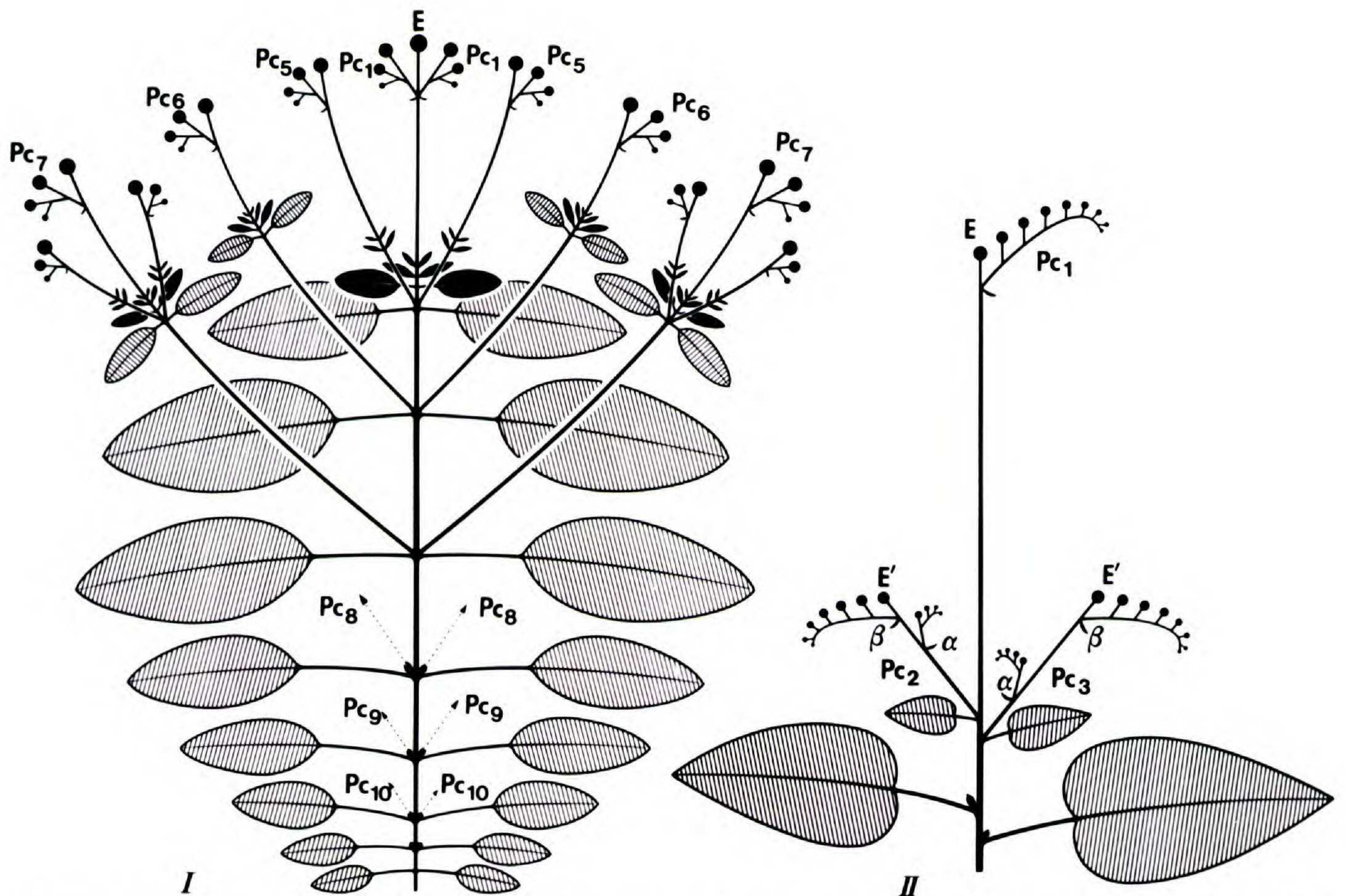


FIGURE 55. *Melastomataceae*. Vertical inflorescence diagrams of *Sonerila margaritacea* (I) and *Bertolonia marmorata* (II). (From Troll.) Pc_1 – Pc_{10} , first through tenth order paracladia; E, terminal flower; E', secondary terminal flower; α , β = prophylls.

versely arranged prophylls are asymmetric, the side pointing outwards (downwards) being larger. The whole paracladial zone comprises two or three pairs of paracladia and is preceded by an inhibition zone, within which only the cotyledonary branches show a slight tendency to unfold. In some way the species resembles *Amphiblemma cymosum* (Fig. 49), which belongs to the same tribe. In *A. cymosum*, however, the flower-bearing system that terminates the shoot comprises about five alternately arranged paracladia. The flowering system of *Sonerila margaritacea* Lindley (Fig. 53 I) is also similar to that of *Calvoa sessiliflora* inasmuch as there are two scorpioid paracladia originating from the axils of a pair of bracts below the terminal flower. The whole "double-scorpioid" is separated from the basal part of the plant by a long and comparatively thin internode. This scape is preceded by three pairs of frondulose to bracteose sterile leaves that form a transition between the preceding foliaceous leaf pairs and the uppermost pair of minute bracts. Since

the preceding pairs of foliage leaves bear paracladia in their axils, the three pairs of sterile leaves form an intercalary inhibition zone within the flowering system. Each of the paracladia pc_5 – pc_7 (pc_2 – pc_4 are missing) in Figure 55 I nearly gives a complete copy of that part of the main stem that follows the point of its insertion, apart from the fact that all of them bear simple scorpioids. In *S. pilosula* Thwaites this also applies to the main axis.

Unlike previous species, *Sonerila rotundifolia* Bedd. (Fig. 52 I) is a rosette plant. The basal part of the main axis bearing the foliaceous rosette leaves is short and vigorous; only the distal part tapers and forms a flower-bearing scape. Since the plant is hapaxanthic, however, the vigorous basal part cannot be termed a rhizome. The umbellike inflorescence that is elevated above the rosette leaves by a long internode consists of two scorpioid paracladia that are inserted below the terminal flower. In *S. scapigera* Dalz. there are more long-peduncled umbellike flowering systems arising from the rosette. The morphol-



FIGURE 56. *Melastomataceae*. *Bertolonia marmorata*.—I. Flowering plant.—II. Same, with most of the rosette leaves removed. (From Troll.)

ogy of this plant has not been clearly elucidated, but we only can confirm that each of the flowering shoots bears its own basal rosette of foliage leaves.

A transitional form that connects *Calvoa sessiliflora* and *Sonerila margaritacea* on the one hand with *Sonerila rotundifolia* and similar species on the other hand is *Bertolonia marmorata* Naudin (Bertolonieae). In this semirosulate plant (Figs. 55 II, 56) the basal leaves are decussate, whereas the cauline leaves change over to alternate arrangement. In the distal part of the main axis there is only one scorpioid paracladium inserted below the terminal flower. Some more paracladia arise from the axils of the frondulose leaves in the lower part of the stem. These paracladia, however, can bear more than one scorpioid. The axillary buds of the upper rosette leaves can also produce paracladia, but most of them remain vegetative. The lowermost axillary buds ordinarily do not develop, nor do they function as innovation buds. Thus the plant is hapaxanthic. Since the scorpioid is formed gradually during anthesis and turns to the direction of the main axis, it can appear as a spike later on.

Eriocnema acaulis Triana, also in the Bertolonieae, seems to resemble *Bertolonia* in its

growth form, but has long-peduncled umbel-like cymoids similar to those in *Sonerila rotundifolia*. On the other hand, *Cinnobotrys oreophila* Gilg (1898, pl. VI), which belongs to the Sonerileae (Jacques-Félix, 1976), bears only one scorpioid paracladium below the terminal flower, which is elevated above the basal rosette by a long internode of the main axis (Fig. 57 II).

Finally *Monolena primulaeflora* Hook. f. may be mentioned here for its very peculiar architecture, which Troll investigated (posthumous manuscript). With regard to the architecture of the primary axis, this plant is similar to *Sonerila rotundifolia*. The main axis is short and vigorous in its basal part, which bears the rosulate foliage leaves. In its distal part the axis tapers and forms a long scape that bears the terminal inflorescence consisting of the terminal flower and one or two scorpioid paracladia. The latter originate in the axils of two broad bracts that fit very well to protect the young flowers. Below these broader bracts there is a pair of smaller bracts that remains sterile. The significant feature of this plant is that it develops plagiotropic paracladia from the axils of the basal foliage leaves. These paracladia are equal to the main axis especially in their vigor. Together with

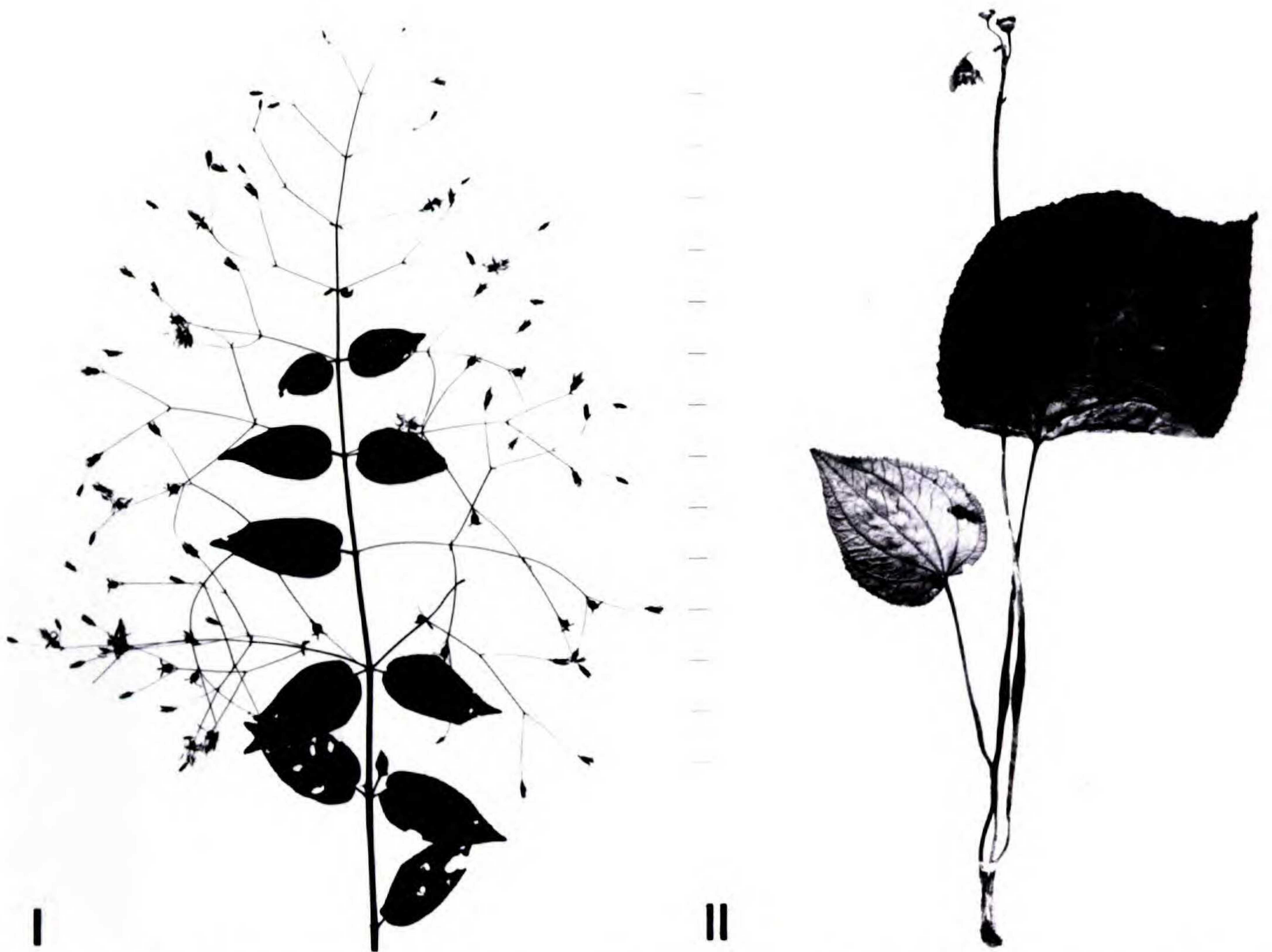


FIGURE 57. *Melastomataceae*.—I. *Nepsera aquatica*; inflorescence. (Brazil. Amazonas: vicinity of Manaus, Prance et al. 11645 (M).) —II. *Cinninobotrys oreophila*; flowering plant. (Tanganjika Territory, distr. Morogoro, Ulugura Mts., Schlieben 2824 (M).)

the bulbous base of the primary axis they form a knobby lump. They remain short, and after the development of foliage leaves, finally taper into a scape bearing an inflorescence. The vigorous basal region of the paracladia can ramify repeatedly and form monochasial or dichasial sympodia. Thus the older plant gives the impression of a multiplicity of foliage leaves and inflorescences that extend and unfold in a centrifugal manner. The character of the plant becomes still more complex because of the anisophylly of the leaf pairs. One may suppose that the vigorous basal paracladia ought to be explained as proleptical innovation shoots.

A difference in size and/or form of paired leaves—commonly called anisophylly (Fig. 58)—already has been mentioned for some taxa. It is typical for a considerable number of species. It ensues from the dorsiventrality

of the plagiotropic axis and is consequently often connected with the development of the axillary shoots (see Troll, 1937: 608). This usually means that the leaves inserted at the underside of the axis are the larger ones (+ leaves), as shown here for *Centradenia grandifolia* (Schldl.) Endl. (Fig. 59 I and the diagram in Fig. 59 II). In *C. inaequilateralis* (Schldl. & Cham.) G. Don and *C. grandifolia*, which have very pronounced anisophylly, only the axils of the (+) leaves subtend axillary shoots. Thus there appear two rows of branches inserted on the underside of the mother axis. This is shown for *C. inaequilateralis* by Figure 59 III, IV. The flowering shoot ends in a terminal flower, which is accompanied by a scorpioid or rarely helicoid paracladium. This arises from the axil of the larger leaf of the small and scarcely anisophyllous leaf pair below the terminal

flower (Fig. 59 V). The paracladia of the preceding leaf pairs differ from this uppermost paracladium by their leafy and more extended hypotagma. They repeat the architecture of their mother shoot by ending in a terminal flower (E') and bearing one scorpioid paracladium (pc') in one of the axils of the distal leaf pair. The effloration of the paracladia proceeds from base to top (Fig. 59 IV). In contradistinction to *C. inaequilateralis*, the paracladia (pc) of *C. grandifolia* (Fig. 54 III) develop flowering second-order paracladia (pc') from the axils of all leaf pairs, and even third-order paracladia (pc''), which are all helicoids.

Generally in anisophyllous species the axillary shoot may be favored or inhibited in the same way as the subtending leaf, or rarely the favored (+) leaf bears a small (-) branch in its axil and the small (-) leaf a vigorous (+) branch. The latter case was described for *Dissotis rotundifolia* (Sm.) Triana by Troll (posthumous manuscript; see Fig. 64 I for explanation).

For the Blakeae (*Topobea* and *Blakea* including *Pyxidanthus*), it was mentioned already that their single flowers are enclosed by an involucre formed by several pairs of bracts. The same applies to some species of *Dissotis* (e.g., *D. rotundifolia*) and many species of *Osbeckia*. In other species of this latter genus the involucre is composed of large pherophylls of some paracladia that are crowded at the ends of the shoots, forming small heads. Often, as in *O. brachystemon* Naudin, *O. chinensis* L., and *O. capitata* Benth. ex Walp., we found the involucre consisting of two leaf pairs which sometimes (in *O. capitata*) included only the terminal flower and one pair of uniflorous paracladia or even only the terminal flower. Many-flowered heads were observed in *O. chinensis*. The dense heads of *Dissotis capitata* (Vahl) Hook. f. (Fig. 60) consist of the terminal flower and one many-flowered monochasial-helicoid paracladium (Troll, posthumous manuscript). In the annual *Nerophila gentianoides* Naudin the involucre is formed by foliaceous leaves.



FIGURE 58. *Melastomataceae*. *Maieta guianensis* Aubl.; anisophyllous branch. (Brazil: vicinity of Pará, Baker 91 (M).)

Well known for its large and showy pink bracts is *Medinilla magnifica* Lindley. This evergreen plant must be regarded as a shrub since it has a basitonic mode of ramification that is conspicuous even when young (Fig. 61 I). The inflorescences contrast sharply with the vegetative parts by the abrupt change of the leaf character and its pendulous position (Fig. 61 II). This position is produced primarily by an active incurvation of the lowermost pedunclelike internode (segregation internode); later it is the weight of the many-flowered inflorescence that keeps it in a hanging position, since the pink-colored segregation internode is very thin. The proximal part of the diplothyrsoid inflorescence bears mostly two pairs of thyrsoid paracladia; in vigorous inflorescences there may be three or even four or five pairs. Sometimes the lowermost pair of bracts remains sterile. The bracts of the lowermost pairs commonly form false tetramerous verticils by an abbreviation of the internode between two dimerous verticils. In the distal and thyrsoid part of the inflores-

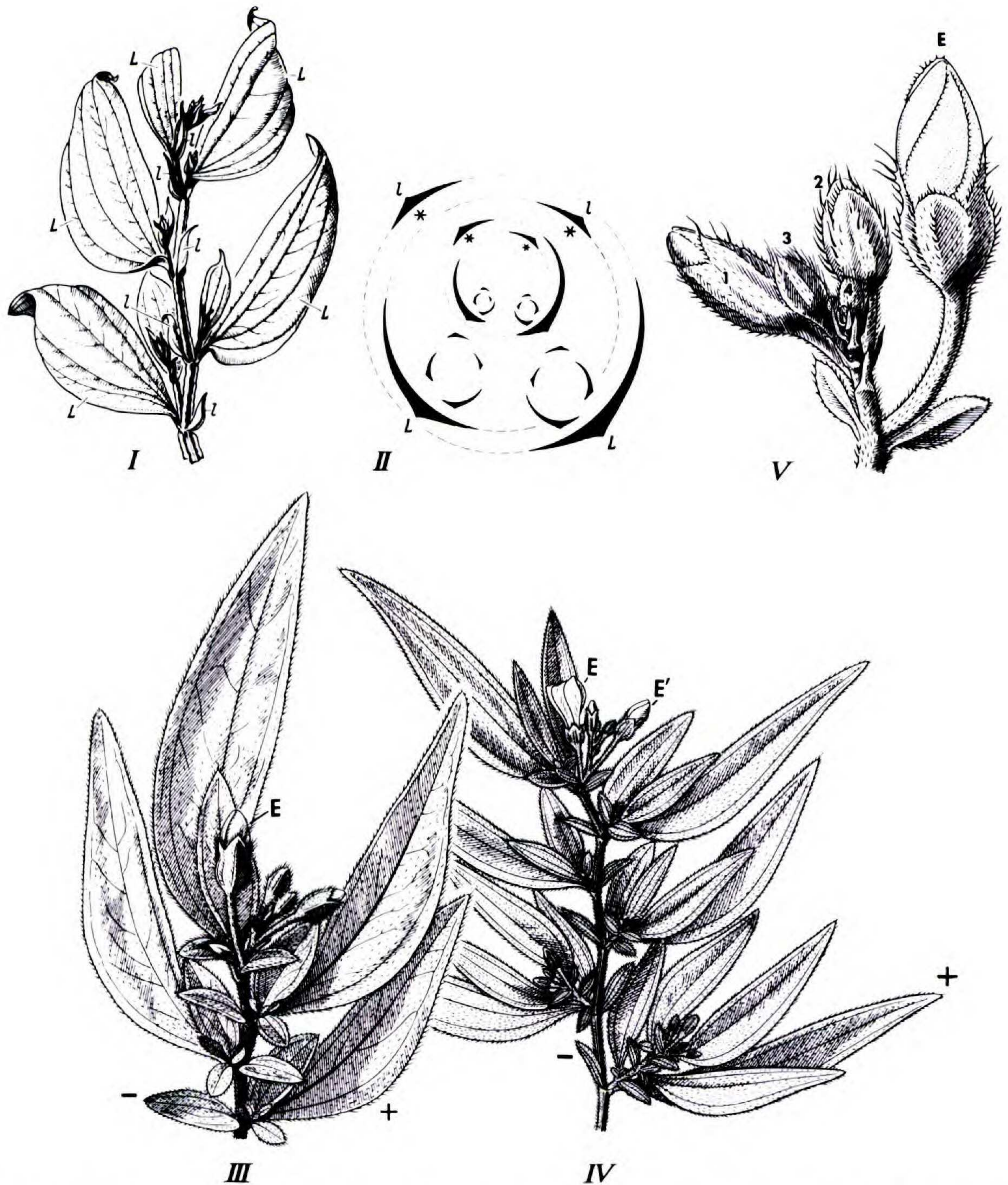


FIGURE 59. *Melastomataceae*. I, II. *Centradenia grandifolia*.—I. Anisophyllous branch.—II. Horizontal diagram; L (as in I), the larger, fertile leaves; l, the smaller, sterile leaves.—III–V. *C. inaequilateralis*; distal part of main shoots with terminal flower (E) and the distal paracladium at the beginning of efflorescence (E' its terminal flower); the small (-) and large (+) leaves.—V. Distal paracladium (pc) with its terminal flower (E) and scorpioid pc. 1–4 = sequence of efflorescence. (From Troll.)

cence the phyllotaxis changes to the formation of proper tetramerous verticils. Sometimes trimerous or hexamerous verticils occur; this also applies to *M. sieboldiana* Planchon. In the distal region of the thyrsoid part of the inflorescence the bracts become smaller and inconspicuous.

The ramification of the paracladia within the thyrsoid region decreases gradually from the formation of maximally seven-flowered cymes in the proximal part to uniflorous par-

acladia in the distal part. The inflorescence can be closed by a terminal flower but often remains indefinite, and the ultimate lateral flowers atrophy (Fig. 64 III). In this case the result is a truncate monotelic synflorescence. If the terminal flower is present, its development is slightly precurrent in relation to the neighboring lateral flowers. Generally the efflorescence of the whole synflorescence is acropetal.

The thyrsoid paracladia at the base of the



FIGURE 60. *Melastomataceae*. *Dissotis capitata*.—I. Shoot with terminal inflorescence.—II. Headlike inflorescence from above. (From Troll.)

inflorescence more or less repeat the structure of the distal part with some alterations due to their lateral position and consequently their dorsiventrality. Their foliation starts with dimerous verticils of large bracts, especially the prophylls, that in their axils can bear thyrsoid paracladia of second order. The whole inflorescence is then a triple thyrsoid.

In the distal part of the thyrsoid paracladia the bracts become smaller. The conformity of the paracladia with the distal thyrsoid part of the inflorescence also refers to the possibility that the apex can atrophy without the formation of a terminal flower.

The inflorescences of *Medinilla sieboldiana* are also pendulous (Fig. 62 I) but differ from those of *M. magnifica* by their very inconspicuous bracts and by the lack of thyrsoid paracladia. The inflorescence thus is a monothyrsoid. It resembles *M. magnifica* in having tetramerous verticils of bracts. In the proximal part the cymose paracladia can

comprise 15 flowers, but distally they are gradually reduced to triads. The development of the terminal flower is conspicuously precurrent to the neighboring lateral flowers. *Medinilla pendula* Merr. is another species with long-peduncled hanging diplothyrsoid inflorescences. There are, however, also species of *Medinilla* with upright inflorescences, as in *M. javanensis* Bl. (Fig. 62 II) and *M. venosa* Bl. (Fig. 63 I). In the latter species and in *M. magnifica* there sometimes occur cauliflorous inflorescences from the axils of leaves that have fallen off already (Fig. 63 II).

Species with proliferating inflorescences are not rare, and some of them show a more or less pronounced tendency to cauliflory. *Medinilla myrtiformis* Triana bears few-flowered botryoids and triadic accessory branches (perhaps even botryoids) in the axils of foliage leaves of proliferating axes. *Medinilla parviflora* Baker and *M. papillosa* Baker are



FIGURE 61. *Melastomataceae*. *Medinilla magnifica*.—I. Basitonic ramification of a young plant.—II. Inflorescence, thyrsoid paracladia. (From Troll.)

similar, the latter showing a slight tendency to cauliflory. In *M. monantha* Merr. the axillary flowering systems are reduced to their terminal flower, which, however, is preceded by two pairs of small bracts. On the other hand, the axillary partial inflorescences of *M. ericarum* Jum. & Perrier are long-peduncled diplothyrsoids.

In *Medinilla ramiflora* Merr., the axillary glomerate thyrsoid flowering systems effloresce when their foliaceous prophylls have fallen off, and *M. tawaensis* Merr. with likewise thyrsoid partial inflorescences is evidently cauliflorous. The same probably applies to *M. clarkei* King.

Medinilla sedifolia Jum. & Perrier, an epiphytic plant with succulent foliage leaves, is another example with proliferating inflorescences. A zone with a few single flowers in the axils of foliaceous leaves is followed by a zone with vegetative axillary shoots (Troll, 1973: 105, who partly refers to W. Rauh).

Probably after a while the main axis can return to the production of lateral flowers again. The foliation of the uniflorous paracladia normally consists only of the scalelike prophylls. Sometimes, however, the prophylls are foliaceous and are followed by two pairs of scales, which in all cases investigated remain altogether sterile.

There is also one case of "epiphyllous inflorescences" reported for the family: *Phyllagathis scortechinii* King, which was investigated by Weber (1982). Among the ca. 35 species of *Phyllagathis* Bl. with essentially terminal "umbel-shaped" or "headlike" inflorescences, *P. scortechinii* is an exception. Its foliage leaves "are posed terminal on woody, axis-like structures ('carriers'), from which they fall off after their life span. Additionally the 'carrier' bears several inflorescences and/or vegetative buds along its upper side" (Fig. 64 II). Weber showed "that this structure is no axis, but a basal, anatomically

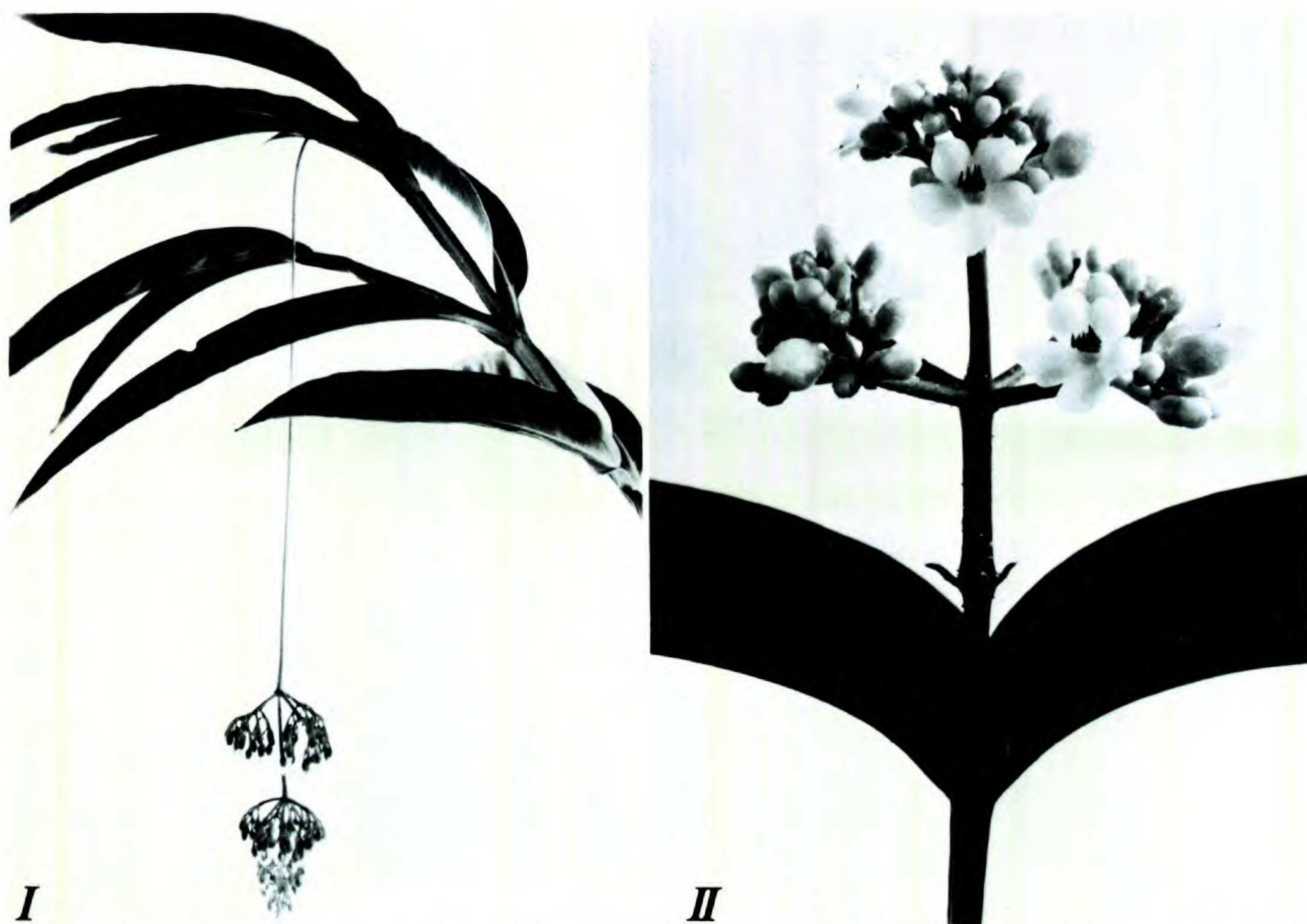


FIGURE 62. *Melastomataceae*.—I. *Medinilla sieboldiana*; shoot with pendulous terminal inflorescence.—II. *M. javanensis*; terminal inflorescence. (From Troll.)

distinctly differentiated part of the leaf, onto which the axillary shoots (multiplied by accessory shoot formation) are displaced.”

PSILOXYLACEAE

Psiloxylon mauritianum Baillon, now recognized to represent a separate family Psiloxylaceae, “has small axillary racemiform inflorescences; these are perhaps anthotelic (botryoids?), but the limited available material (all dried) is insufficient to determine whether the apparently terminal flower is indeed truly so. Disperse phyllotaxy in the inflorescence (as well as in vegetative regions) and general recaulescence of the bracts increase the difficulty of interpretation.” We cannot add much to this statement given by Briggs & Johnson (1979: 181) for the same reason: scantiness of material. It does appear, however, that there is no terminal flower. In this case the inflorescence could be termed a bot-

rytic florescence. According to our observations, the flowers are subtended by bracteous pherophylls and bear bracteous prophylls. In the material investigated (Fig. 65) the flower-bearing systems are brachyblasts reduced to their florescence and inserted on older axes. Thus the plant might be called cauliflorous.

MYRTACEAE

In Myrtaceae, the “central type” and perhaps the phylogenetically primitive form of inflorescence is a monotelic thyrsoid (i.e., a thyrsoic inflorescence with terminal flower) or panicle terminating a leafy shoot. Inflorescences of this type can be found among the Myrtoideae (species of *Syzygium* and *Eugenia*) and the Leptospermoideae (species of *Metrosideros*, *Eucalyptus*, and *Angophora*), and they are characteristic of the Heteropyxidoideae (*Heteropyxis natalensis* Harvey, Fig. 66; see also Weberling, 1963). A



FIGURE 63. *Melastomataceae*. *Medinilla venosa*.—I. Terminal inflorescence.—II. Cauliflorous inflorescences. (From Troll.)

typical monotelic inflorescence is exemplified by *Syzygium aromaticum* (L.) Merr. (Figs. 67, 68 I). The inflorescence axis ends with a terminal flower. This also applies to all floral branches below the terminal flower. All these branches, whether branched or not, are homologous and all are referred to by the term *paracladia*. Accordingly the ramifications of these *paracladia* are called *paracladia* of second to n^{th} order (pc' , pc'' , . . .).

As is well known, the complexity of such an inflorescence, that is, the degree of ramification of the *paracladia* and the extension of the enrichment zone, may be modified to a certain extent in the same species. On the other hand, the differences in complexity may be a distinguishing character between different taxa. Thus in contrast to *Syzygium aromaticum*, in *S. paniculatum* Banks & Gaertner (Fig. 67) the *paracladia* of first order are

uniflorous throughout (Troll, 1969: 258). This results in the formation of a botryoid. In this species, reduction may even go further until only the terminal flower remains.

In *Syzygium aromaticum*, frequently in *S. paniculatum*, as well as in many other *Myrtaceae*, a pair of sterile bracts (*metaxephylls*, *Zwischenblätter*) preceding the terminal flower can be observed. In *S. paniculatum* they may be replaced by more foliaceous leaves that bear single-flowered (monadic) *paracladia* in their axils (Troll, 1969: 258–259).

In *Eugenia lanceolaria* Roxb. (now *Syzygium lanceolarium*) and *E. macrocarpa* Roxb. (*Syzygium macrocarpum*) the usual form of the inflorescence seems also to be a botryoid, whereas in *S. thumra* (Roxb.) Merr. & Perry the ramification of the floral branches is increased (Fig. 69). To a certain extent

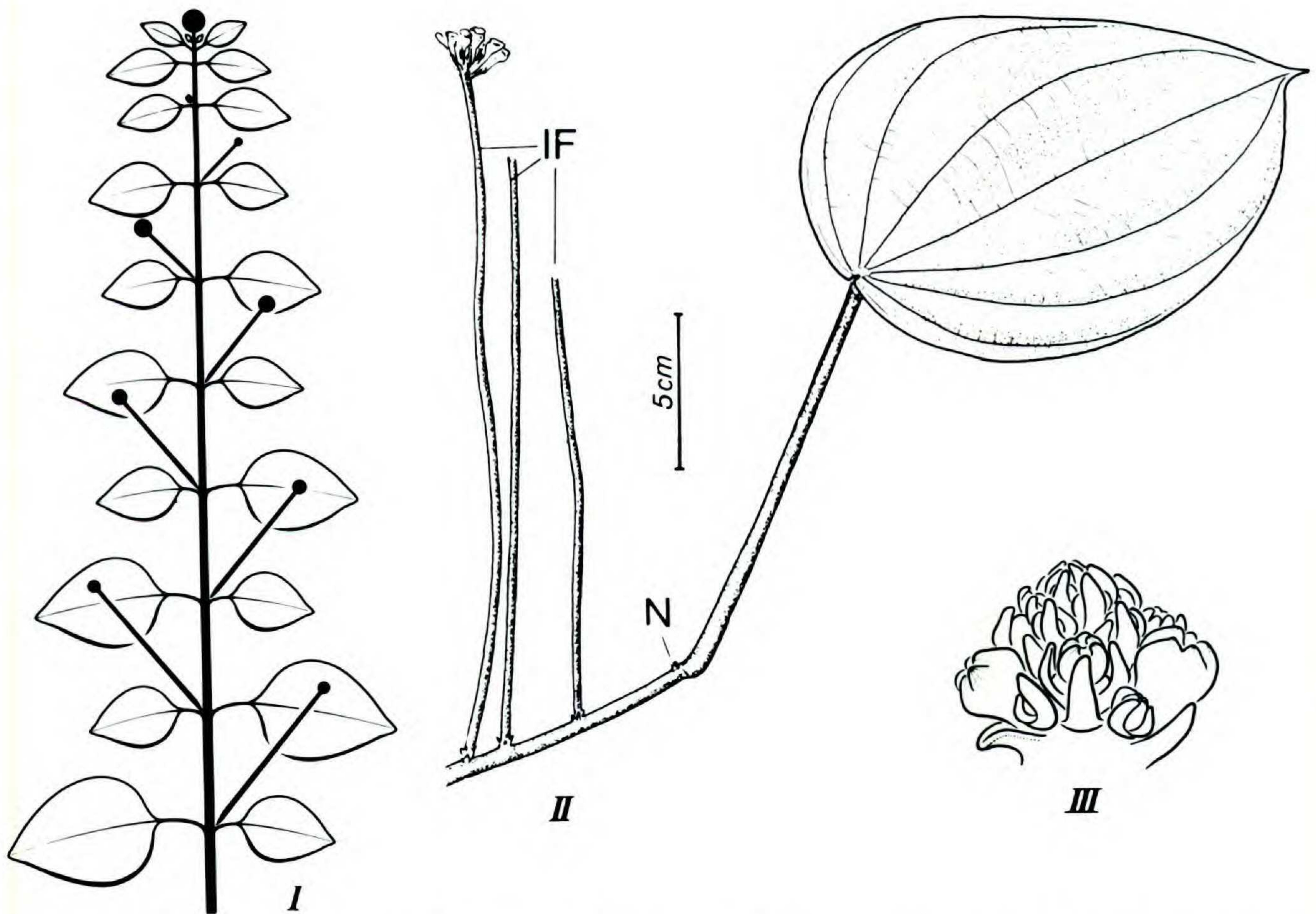


FIGURE 64. *Melastomataceae*.—I. *Dissotis rotundifolia*; vertical diagram of an anisophyllous flowering shoot.—II. *Phyllagathis scortechinii*; "carrier" with foliage leaf and some (partly incomplete) inflorescences/infrutescences (IF) and leaf scar (N).—III. *Medinilla magnifica*; inflorescence apex in state of truncation. (I, III from Troll; II from Weber, 1982.)

this is due to a high degree of cymose branching, which means a consecutive ramification from the axils of the prophylls. An inflorescence with the main axis bearing lateral cymes is defined as a thyrsoid; in this sense the inflorescence of *S. thumra* as well as of *Heteropyxis* (Fig. 66) is a pleiothyrsoid.

As already shown by the few species mentioned here, the foliation of the flower-bearing system may consist of bracts only (bracteose), or there may be a transition from foliage leaves at the base to distal bracts (frondobracteose), or the foliation may be leafy throughout (foliose, frondose). The latter applies to the inflorescence of *Syzygium acuminatum* (Roxb.) Miq. (Fig. 70). This inflorescence also presents another feature that is significant for many Myrtaceae: the main axis of the inflorescence is not closed by a terminal flower but ends in a bud (*blastotelic* in the sense of Briggs & Johnson, 1979: 176). Nevertheless, all of the paracladia, including those with more than one pair of flower-bearing

branches, are provided with terminal flowers, thus demonstrating the monotelic character of the inflorescence (Troll, 1969: 255; Radlkofer, 1890: 184).

The close morphological relations between these different forms of monotelic inflorescences becomes evident by the comparison of closely related taxa, as among the various species of *Metrosideros* sensu lato that Dawson (1968) investigated. Among these, *M. albiflora* Sol. ex Gaertner (Fig. 71 I) has a bracteose (thyrsopaniculate) inflorescence, and *M. carminea* W. Oliver (Fig. 71 II) a frondose diplobotryoidal inflorescence; both still terminate in an apical flower. As a result of further reduction, the inflorescence of *M. diffusa* Sm. (Fig. 71 III) consists of several densely contracted pairs of triadic paracladia only but still ends in a terminal flower. In the similar inflorescence of *M. perforata* A. Rich. (= *scandens* Sol. ex Gaertner?), the terminal flower is replaced by a vegetative bud (Fig. 71 IV). Moreover, in the loose inflorescences



FIGURE 65. *Psiloxylaceae*. *Psiloxylon mauritanicum*. (Mauritius: 1825, Sieber s.n.; *Fl. Maurit. II*, No. 123; G.)

of *M. kermadecensis* W. Oliver (= *M. polymorpha* Hook.?), not only the terminal flower closing the inflorescence axis, but also those of the paracladia of first order are replaced by buds (Fig. 71 V). The same applies to *M. umbellata* Cav. (= *M. lucida* A. Rich.?) with more contracted (Fig. 71 VI) or reduced inflorescences (Fig. 71 VII).

Similar differences can be found among species of *Angophora*. While in *A. hispida* (Sm.) Blaxell, *A. floribunda* (Sm.) Sweet, *A. costata* (Gaertner) Britt., *A. melanoxylon* Bak., and *A. subvelutina* F. Muell. the main axis of the (thyrso-)paniculate inflorescences is closed by a terminal flower, the thyrsopanicula of other species end in a bud.

These terminal buds, which appear "to consist of vegetative rather than floral organs," become abortive in many cases (the inflorescence being *anauxotelic* in the sense of Briggs & Johnson, 1979: 176). In many

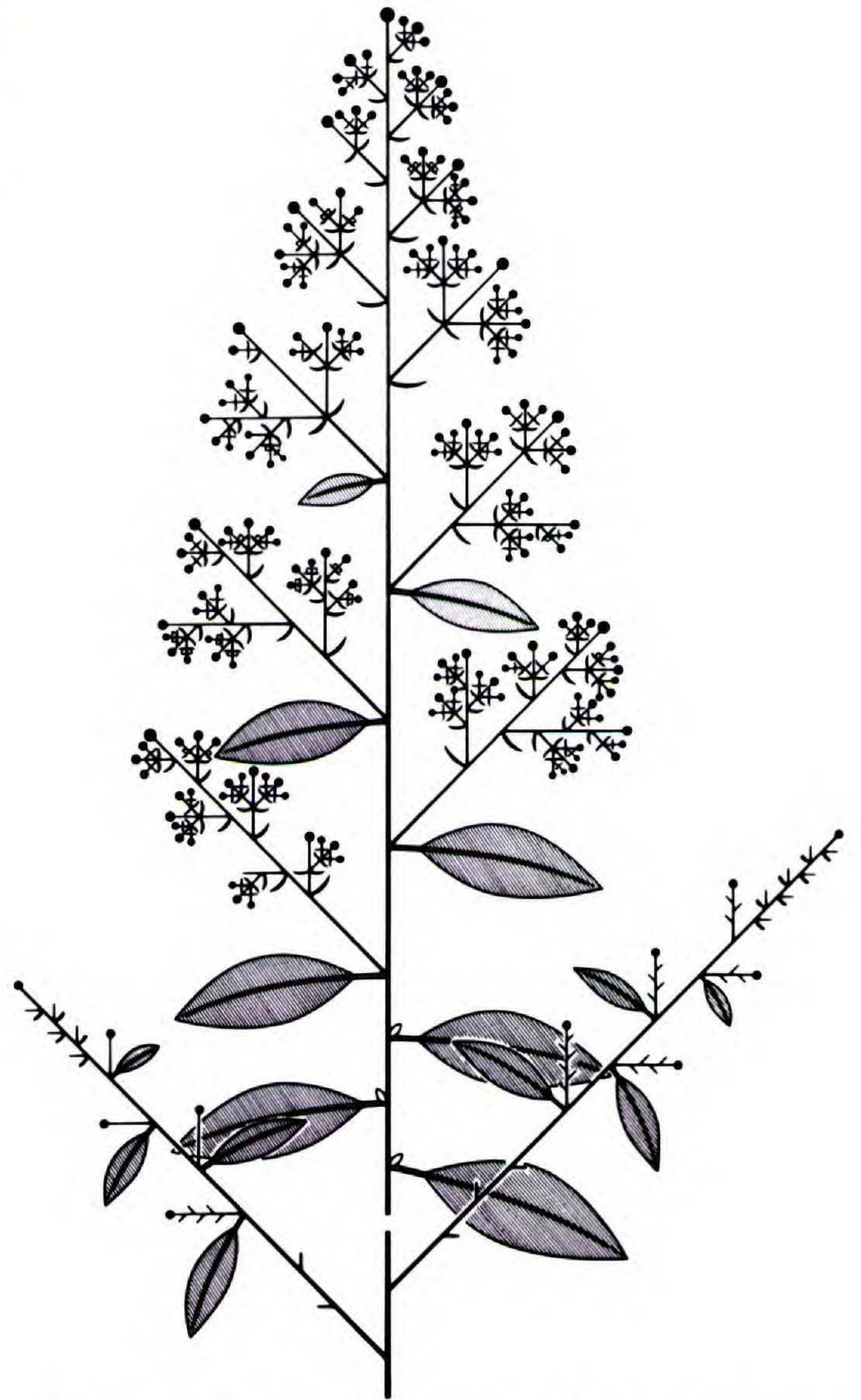


FIGURE 66. *Heteropyxidaceae*. *Heteropyxis natalensis*; diagram of a flowering shoot. At the interruption of the main axis three foliaceous leaves and their internodes have been omitted, and the ramification of the vigorous basal branches was not carried out in detail. (South Africa: koppie in the area of the University of N. Transvaal, Weberling 7644.)

other cases sooner or later the terminal bud continues growth beyond the flowering region, producing a vegetative shoot (for inflorescences of this kind the term *auxotelic* is used by Briggs & Johnson, 1979). In *Angophora costata*, Briggs & Johnson (1979, fig. 6b, c) observed inflorescences closed by a terminal flower ("anthotelic" inflorescences) as well as those ending in a terminal bud, which sometimes aborted and sometimes continued growth. The inflorescence of *A. subvelutina* was found with a terminal flower (Briggs & Johnson, 1979), while Troll (unpubl. data) found a terminal bud continuing growth in the same species. Thus especially within *An-*



FIGURE 67. *Myrtaceae*. Inflorescences.—Left. *Syzygium aromaticum* (from Köhler, 1923).—Right. *S. paniculatum*. (From Troll.)

gophora (and in some other taxa of the *Eucalyptus* alliance) a high degree of flexibility in the formation of terminal flowers is revealed.

Dawson (1968: 48) pointed out that in those species of *Metrosideros* that bear terminal buds, the “bud is inactive during flowering, but may later develop into a leafy branch.” As will be shown later, however, the moment in which the apical vegetative bud turns to continue growth may be sooner or later.

The reversion of the inflorescence apex to vegetative growth, commonly called *proliferation* (Troll, 1959a: 116), is characteristic for many *Myrtaceae*, perhaps even for the majority of species.

Parkin (1914: 556) regarded proliferating inflorescences as a separate type of inflorescence, which he called “intercalary inflorescences,” because “the flower-bearing part of

the axis is . . . intercalated between two foliage-bearing portions.” In using this term he especially referred to the Australian (or prevalent Australian) genera *Callistemon*, *Melaleuca*, and *Metrosideros*. Indeed the appearance of the flowering shoots of *Melaleuca* (Fig. 72) and *Callistemon* (Fig. 72) suggest this term, all the more as the process of the formation of a terminal inflorescence and proliferation can recur in regular intervals of development, mostly in connection with climatic factors.

We must emphasize, however, that there are many taxa (e.g., *Veronica*, *Lysimachia*, several ligneous *Melastomataceae* or *Rubiaceae*) that include species with terminal bracteose and terminal foliose inflorescences as well as species with proliferating leafy inflorescences. Often these forms are connected by continuous series of intermediate forms. Thus the so-called “intercalary inflores-

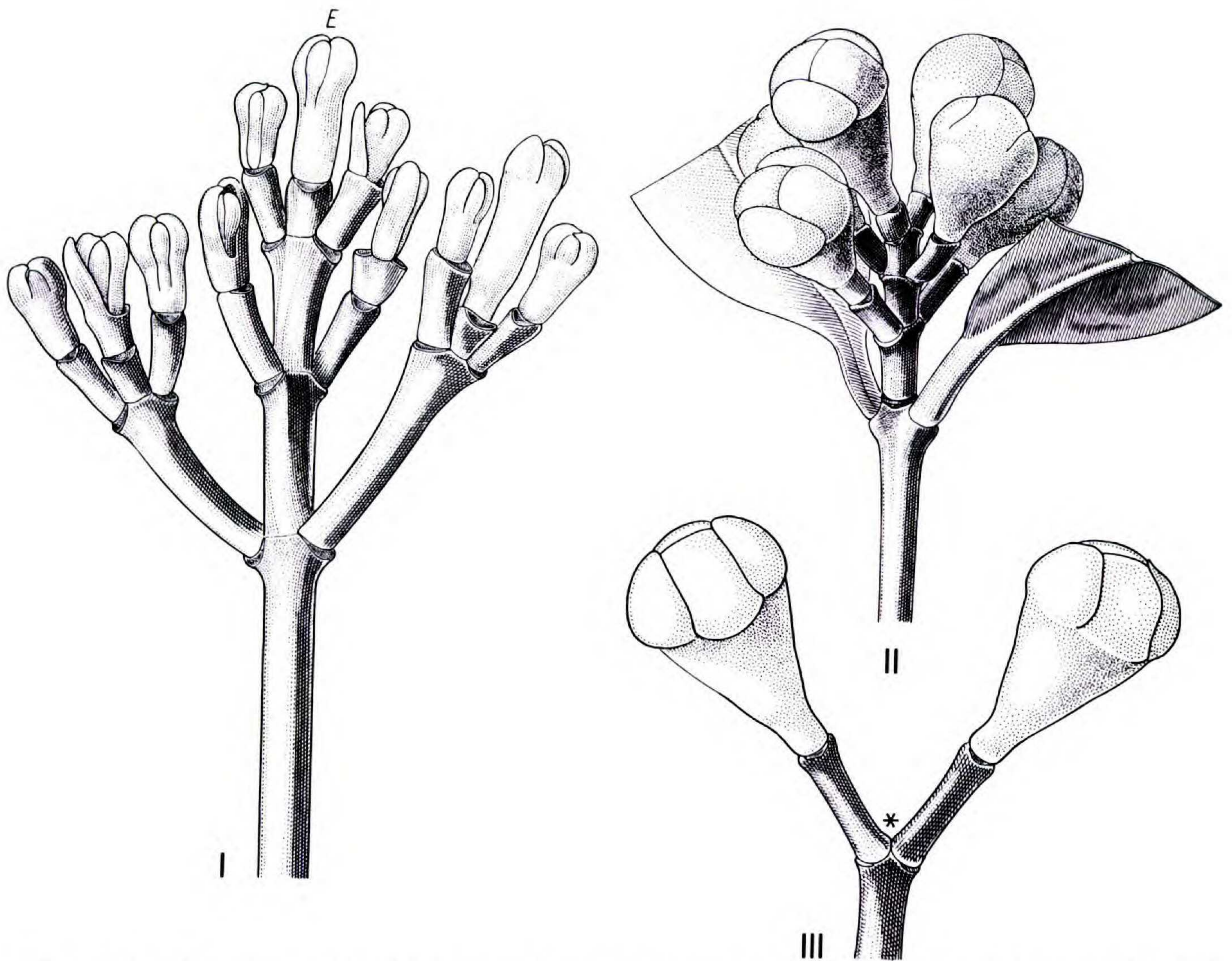


FIGURE 68. *Myrtaceae*.—I. *Syzygium aromaticum*; few-flowered inflorescence, the bracts fallen off. II, III. *S. jambos*.—II. Inflorescence, the terminal flower aborted (truncate monotelic synflorescence).—III. Distal part of the inflorescence in detail. Asterisk indicates place of the aborted terminal flower. (From Troll.)

cences” are regarded as derived from the terminal ones.

The fact that the development of flower-bearing systems and vegetative zones occurs successively in the same shoot, which continues growing over a long time, may prove to be favorable under certain conditions, especially for plants with enduring leaves.

In the examples mentioned above, the proliferation takes place after or during the efflorescence of the inflorescence. The efflorescence, however, may be delayed somewhat more while the shoot apex reverts to vegetative growth and may even form branches, as in *Beaufortia decussata* R. Br. (Fig. 73 II).

In such cases the normal zonation in the flowering systems of monotelic as well as of polytelic character (Fig. 3) seems to be reversed, since the continuation of the vegetative ramification system takes place above

the flower-bearing zone. On the other hand, the extreme retardation of formation and anthesis of the flowers may result in different manifestations of cauliflory. Thus in *Calothamnus rupestris* Schau. and *C. villosus* Ait., anthesis can be delayed so long that the resting flower buds are occluded by peridermal tissue.

The degree of ramification of the flower-bearing systems can be very different, and this applies to proliferating inflorescences as well as to nonproliferating inflorescences. Thus in the proliferating inflorescence of *Pimenta dioica* (L.) Merr. (Fig. 74), *Gomidesia hookeriana* Berg, *Krugia ferruginea* (DC.) Urban, or *Calyptrocalyx chytraculia* (L.) Swartz, the partial inflorescences that originate from the axils of foliage leaves are highly ramified and present themselves as thyrsoidean systems. In contrast to the leafy

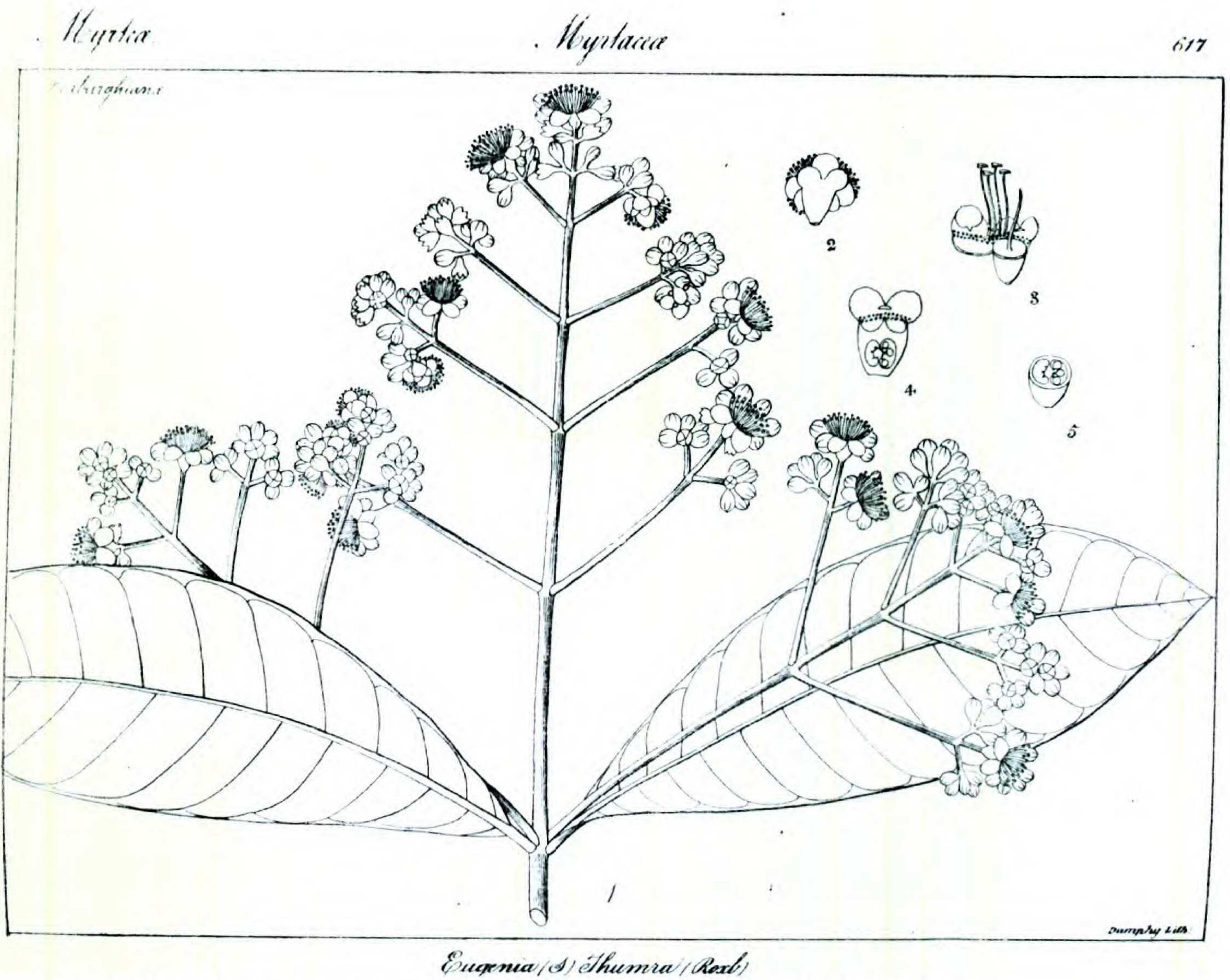


FIGURE 69. Myrtaceae. *Syzygium thumra*; flowering branch. (From Wight, 1843.)

main axis, they end in a terminal flower, thus revealing the monotelic character of the whole inflorescence. The same applies to some species of *Marlierea* and *Myrcia*, which produce more or less ample ramified thyrsoid-paniculate paracladia, whereas other species of these genera, as well as *Mitranthes egersii* and *Myrrhinium loranthoides* (Cabrera, 1978: 78), only bear simple thyrsoids in the axils of foliage leaves.

A high degree of flexibility in the alternative formation of terminal flowers or terminal auxotelic or anauxotelic buds is represented by *Decaspermum paniculatum* Lindley. As reported by Briggs & Johnson (1979: 187) "the second-order and higher-order axes may produce: a) both terminal and lateral paniculate shoots . . . or b) lateral paniculate shoots only, the apical bud retaining

the capacity for continued growth." Figure 75 I, which illustrates the results of Briggs & Johnson, resembles Figure 75 II, reporting our own results. The somewhat contradictory examples of inflorescence structure, however, can be elucidated in an acceptable way as being derived from a monotelic thyrsoid-paniculate base type. In *D. parviflorum* Kurz, we observed an indeterminate main axis bearing axillary loosely branched monothyrsoids with slightly disperse phyllotaxy.

Figure 75 I and II also represents examples of the development of *accessory branches*. Within the Myrtaceae these accessory branches are mostly phylloscopic. They occur as single accessory flowers (Fig. 75 I, II), triadic branches (Fig. 75 I), or even as botryoids (Fig. 75 I) and perhaps also as thyrsoids. Sometimes several accessory axes in a

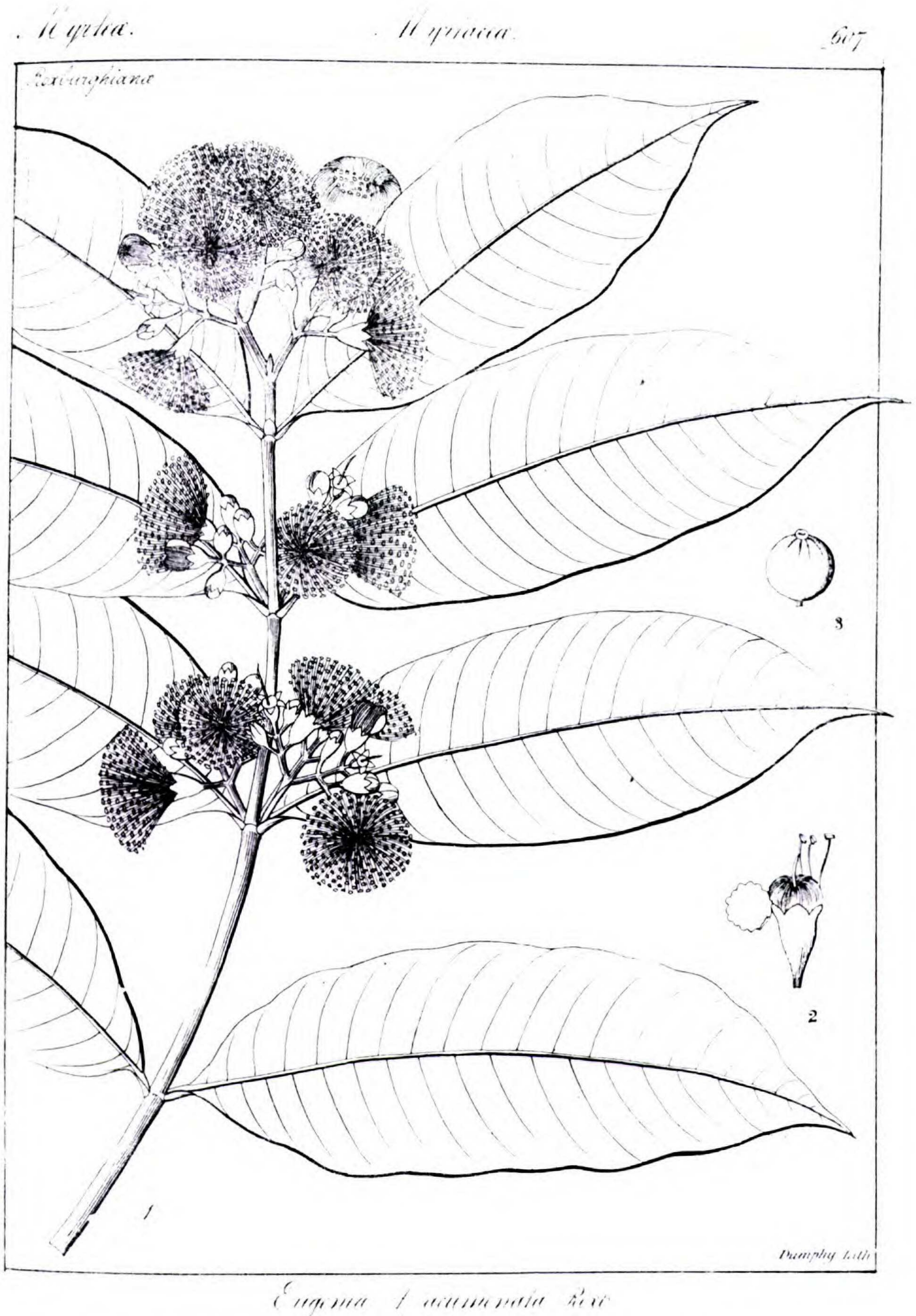


FIGURE 70. *Myrtaceae*. *Syzygium acuminatum*; flowering branch. (From Wight, 1843.)

vertical series are developed in the same axils. In this case they may be different in their degree of ramification or not, both demonstrated in *Myrceugenia exsucca* (DC.) Berg (Fig. 80 IX).

Within the large genus *Eucalyptus*, terminal thyrsoid-paniculate inflorescences ending in a terminal flower as well as proliferating inflorescences can be observed. Although some sections of the genus may exclusively follow

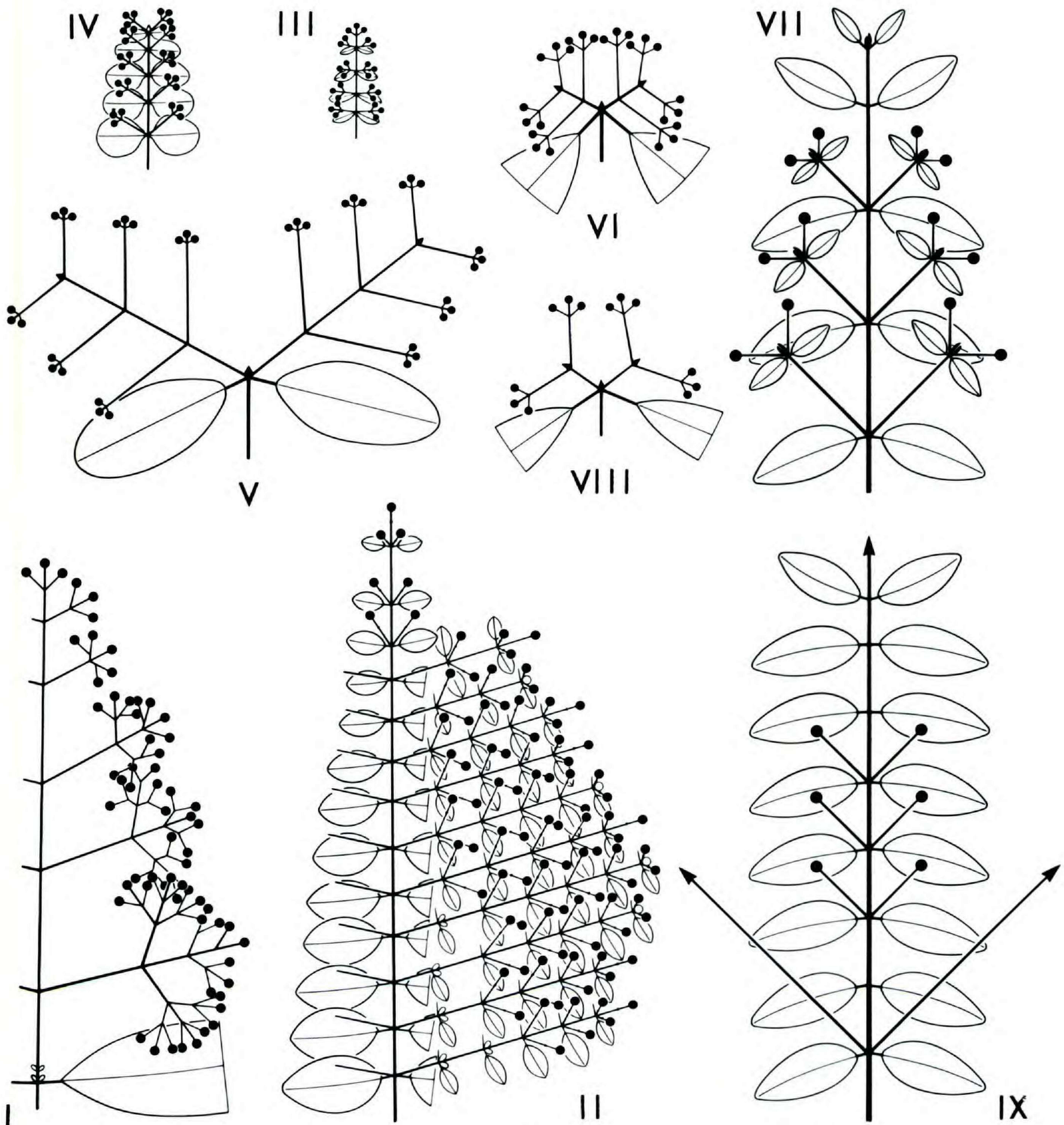


FIGURE 71. *Myrtaceae*. Inflorescence diagrams.—I. *Metrosideros albiflora*.—II. *M. carminea*.—III. *M. diffusa*.—IV. *M. perforata*.—V. *M. kermadecensis*.—VI, VII. *M. umbellata*.—VIII. *Rhodomyrtus tomentosa*.—IX. *Acca sellowiana*. (I–VII from Dawson (1968) with some graphical alterations; bracts were omitted by Dawson.)

one or the other mode, even closely related species can be different in this respect. Thus in many species of sect. *Adnataria* of subg. *Symphyomyrtus* (Pryor & Johnson, 1971), the main axes of the inflorescences were found to have terminal flowers (*E. melliodora* A. Cunn., *E. paniculata* Sm. (Fig. 76 I), *E. polycarpa* F. Muell., *E. polyanthemos* Schau., *E. populnea* F. Muell., *E. pruinosa* Schau. (Fig. 76 II), while others (e.g., *E. sideroxylon* A. Cunn.) have a proliferating main axis. In still others (e.g., *E. intertexta*

R. T. Baker) inflorescences with terminal flowers and proliferating inflorescences were even found on the same herbarium sheet (Penfold & Willis, 1961, pl. 38, fig. 6). According to Johnson (1972: 23, fig. 5) this form "has adaptive significance" and is derived from forms without a terminal flower (the reverse seems more probable).

The partial inflorescences are condensed cymes (Fig. 75 III, IV), which often are described as umbels but more correctly should be called umbellasters (Johnson, 1972; Briggs



FIGURE 72. *Myrtaceae*. I, II. *Melaleuca decora*; inflorescence before (left) and after (center) proliferation.—Right. *Callistemon rigidus*; proliferating shoot after anthesis, with fruits of preceding flowering phase. (From Troll.)

& Johnson, 1979) or sciadioids (Troll, 1964: 53).

The number of flowers in such umbellasters can be seven or more, but often their number is reduced, and they are not rarely uniflorous (*Eucalyptus globulus* Labill., *E. tetraptera* Turcz.). They can show significant characters, such as concrecence of their gynoecia in *E. lehmannii* (Schau.) Benth. or broadening of the hypopods, especially in *E. platypus* Hook. (Fig. 77). In *E. cinerea* F. Muell. (Fig. 73), *E. macrorhyncha* F. Muell., and other species with proliferating inflorescences, a strong delay of anthesis as already noted for *Beaufortia decussata* takes place. As a consequence the top of the inflorescence axis may produce vegetative branches while the partial inflorescences at its base are still in flower. The connection of these conditions with the formation of cataleptic (Müller-Doblies & Weberling, 1984) flower-bearing short

shoots and with cauliflory seems to be obvious here.

Frequently the flower-bearing branches are reduced to botryoids, as in *Myrciaria floribunda* (Willd.) Berg (Cremers, 1983/1986, fig. 42/7) or *Eugenia guatemalensis* Cogn. In species of *Blepharocalyx* (*B. tweedii* Hook. & Arn., *B. gigantea* Lillo, cf. Cabrera, 1978, fig. 143; Digilio & Legname, 1966, fig. 82) or *Backhousia myrtifolia* Hook. & Harvey, the paracladia are long-stalked and loosely branched, seven- to five-flowered cymes. This reduction of the paracladia goes even further to form long-stalked, loosely branched triads, as in *Myrcianthes cisplataensis* (Camb.) Berg, *Myrceugenella apiculata* (DC.) Kausel, or *Eugenia pseudo-mato* Legr. (Digilio & Legname, 1966, figs. 84, 87) or to long-stalked, biflorous or uniflorous (monadic or dyadic) paracladia still with prophylls (*Eugenia pungens* Berg; Digilio &

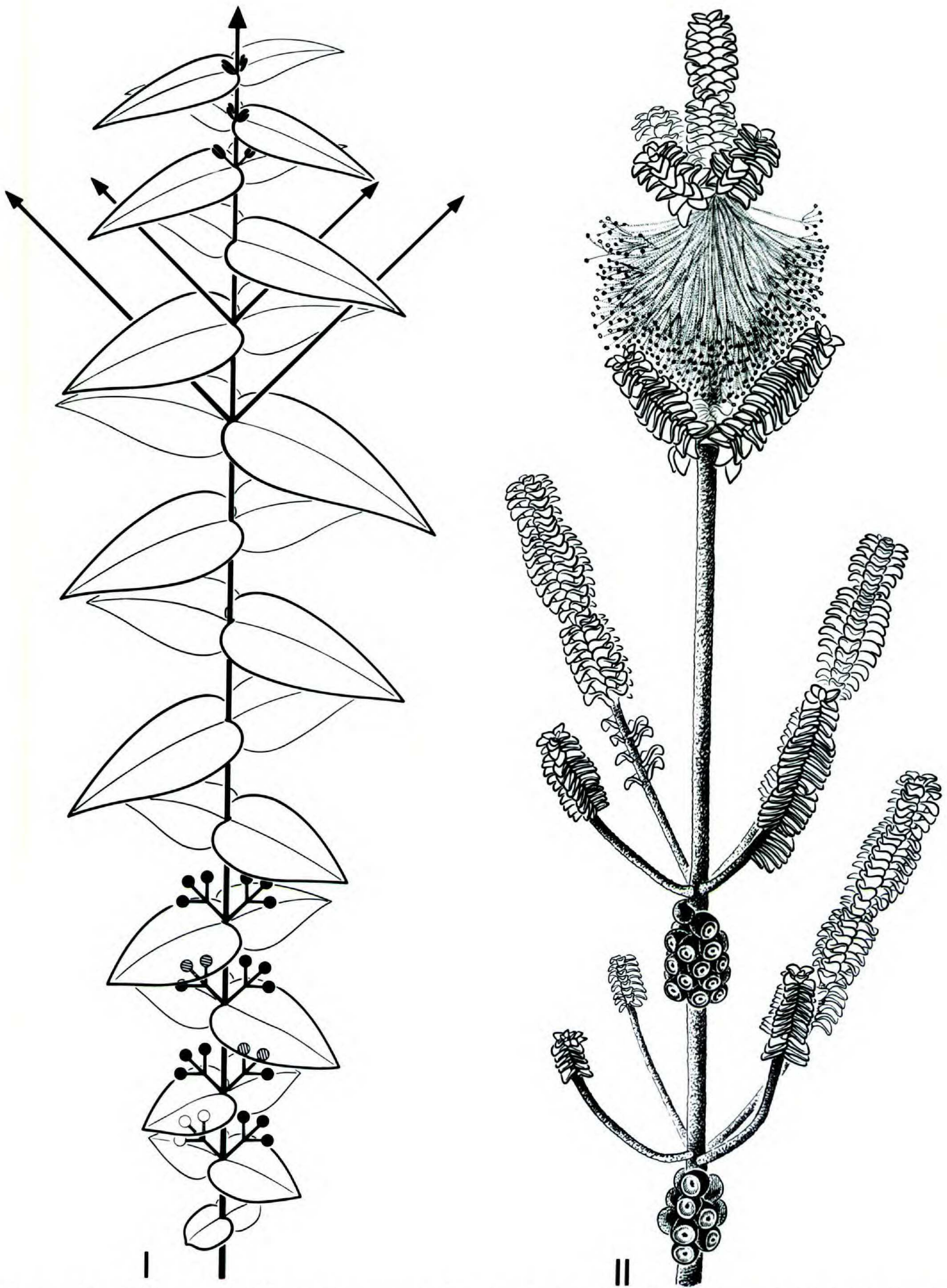


FIGURE 73. *Myrtaceae*.—I. *Eucalyptus cinerea*; diagram of a flowering shoot. The proliferating inflorescence axis already had developed branches when anthesis had started (Weberling 7413).—II. *Beaufortia decussata*; flowering shoot with fruits of preceding flowering phases.



FIGURE 74. *Myrtaceae*. *Pimenta dioica*; inflorescences.—Left. Proliferation has taken place already.—Right. The inflorescence axis still ends in a bud. (From Troll.)

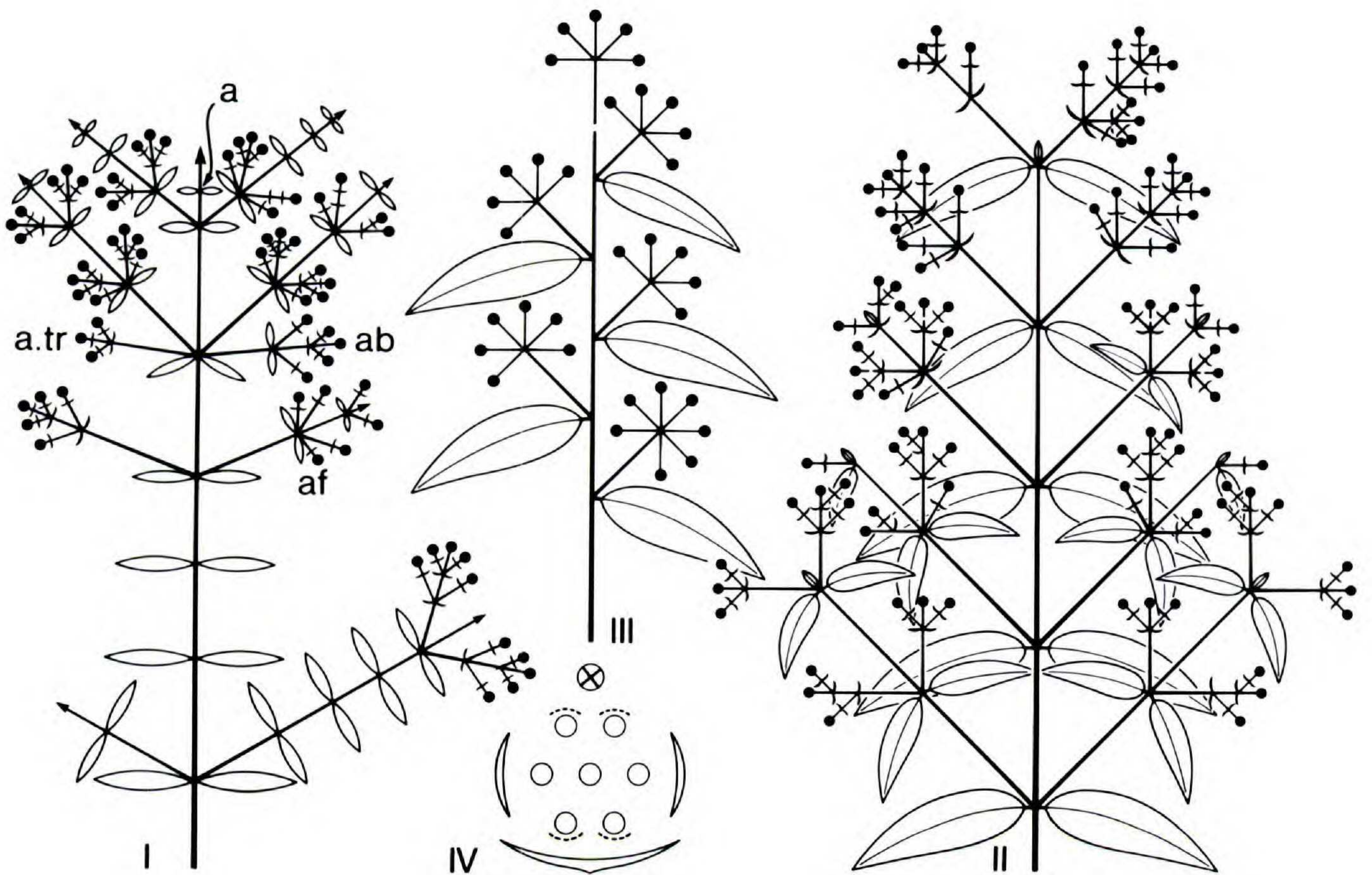




FIGURE 76. *Myrtaceae*.—I. *Eucalyptus paniculata*.—II. *E. pruinosa*; flowering branches. (From F. Mueller.)

Legname, 1966, fig. 85). Condensed and sessile triadic or uniflorous paracladia compose the spikelike proliferating inflorescences so characteristic of many species of *Calothamnus*, *Callistemon* (triadic pc in *C. suberosum* only; Dawson, 1978a, fig. 3), *Melaleuca* (Fig. 72), and *Beaufortia* (Fig. 73 II).

Leafy proliferating botrya are characteristic for all or many species of the myrtoid genera *Ugni*, *Myrtus*, *Fenzlia*, *Psidium*, *Myrceugenia*, *Luma*, *Acca* (Fig. 71 IX), and others and of the leptospermoid genera *Eremaea*, *Baeckea*, *Balaustion*, *Calythrix*, *Wehlia*, *Pileanthus*, *Thryptomene*, *Micromyrtus* (Fig. 78 III, IV), *Verticordia* (Fig.

78 I, II), *Regelia* (also triadic pc?, cf. Briggs & Johnson, 1979), and others.

In many species of *Kunzea* (e.g., *K. capitata* Reichb. and *K. ericifolia* Reichb., Fig. 79 I), the botrytic or spikelike inflorescences are capitate, as in species of *Agonis* (Fig. 80 II) and *Sinoga*.

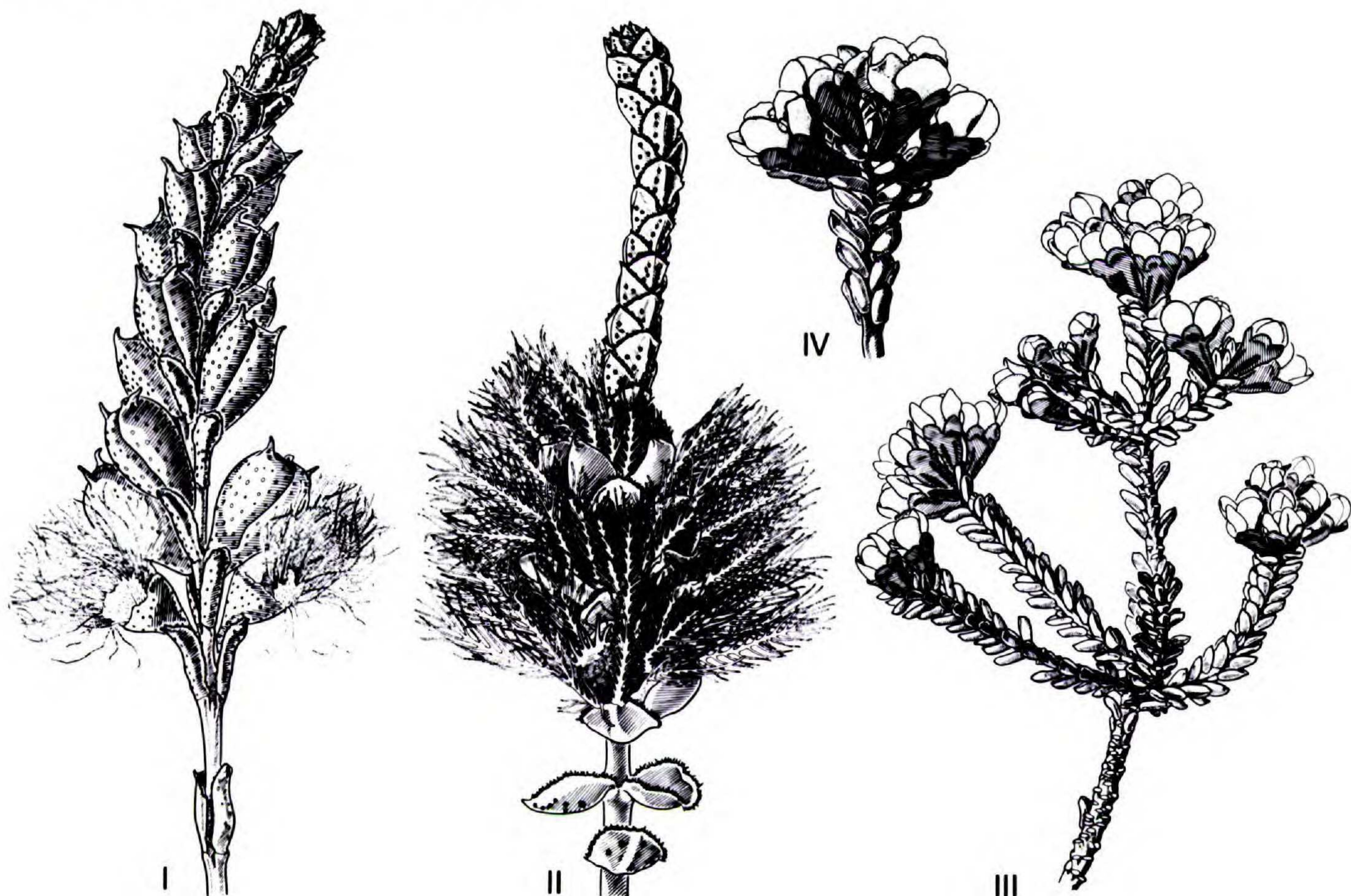
The agglomeration of flowers into showy heads decidedly supports the attraction of pollinators. This is especially true for the pseudanthial inflorescences of *Darwinia* and *Actinodium*. In both, the dense heads are botrya that can proliferate after flowering (especially in *Darwinia*, Fig. 81). In *Darwinia* the subtending leaves of the flowers are inconspic-

←
FIGURE 75. *Myrtaceae*. I, II. *Decaspermum paniculatum*.—I. Flexibility of inflorescence development (from Briggs & Johnson; showing the actual branching of a herbarium specimen: Castlewood, Johore, Malaysia; NSW 13876).—II. Diagram of the inflorescence of another herbarium specimen (Khasia: Hooker s.n. (M)). III, IV. *Eucalyptus intertexta*.—III. Inflorescence drawn from herbarium specimen (Australia. New South Wales: Byrock, Oct. 1903, J. L. Boorman s.n. (M)). In another inflorescence represented on the same sheet, the apex was proliferating.—IV. Diagram of a partial inflorescence ("umbellaster"). a, apex of blastotelic main axis; a.tr, accessory triadic branch; ab, accessory botryoid; af, accessory flower. (IV From Troll.)



Herb. n. 1000
W. F. Faure
Zugängen 1918

FIGURE 77. *Myrtaceae*. *Eucalyptus platypus*.—Left. Herbarium specimen.—Right. Detail. (Algeria: Oran à Santa Cruz, 9.5.1918, A. Faure s.n. (M).)



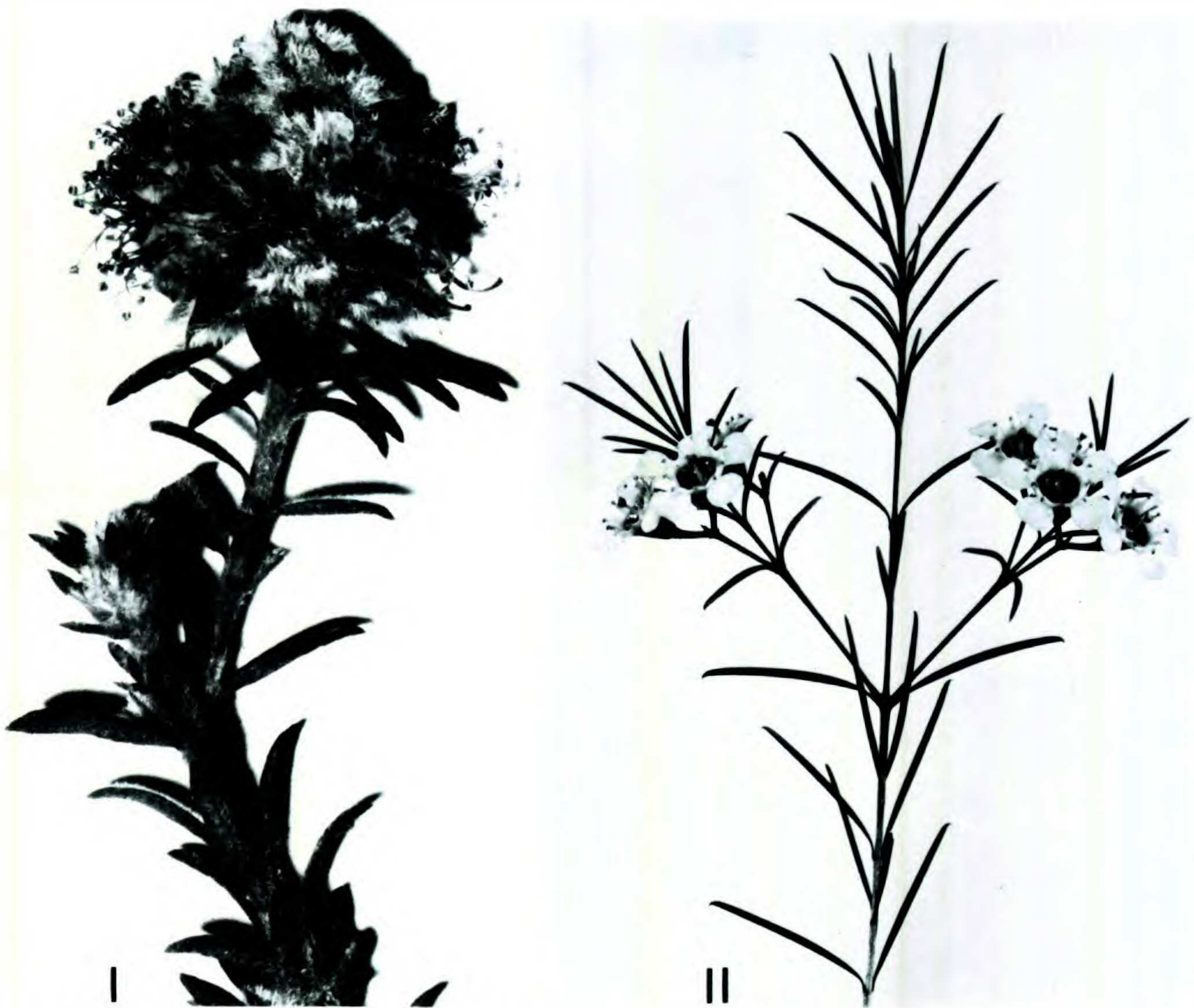


FIGURE 79. *Myrtaceae*.—I. *Kunzea ericifolia* (Meebold 11881).—II. *Chamelaucium uncinatum*; flowering branch. (II From Troll.)

uous, but the adjacent leaves are often greatly enlarged, petaloid, and colored, giving the capitate inflorescence a flowerlike shape (Fig. 82). For the western Australian species, Briggs & Johnson (1979: 201) found “a sequence from (for example) the little-modified *D. thymoides* Benth., through *D. virescens* (Meissn.) Benth., where the petaloid leaves are about as long as the perigynia (‘floral tubes’), to the pendulous ‘bells’ . . . of *D. meeboldii* C. A. Gardn. (‘Mondurup Bell’) or *D. speciosa* (Meissn.) Benth., in which individual flowers are hidden by several series of long petaloid leaves,” and the inflorescence axis “is an-auxotelic” (Figs. 80 IV, 82). In *Actinodium*

cunninghamii Schau. ex Lindley, the “daisy-like” flower heads have several rows of “rays” formed by modified sterile flowers (Figs. 80 V, 82). The axis of the capitulum “is somewhat swollen but not flat, and variation in the length of the peduncles of the monads brings the flowers to approximately the same level, although the outermost arise c. 2–5 mm below the innermost” (Briggs & Johnson, 1979: 202).

It is not rare that the development of triadic to uniflorous paracladia and the arrangement in leafy thyrse, botrytic or spikelike proliferating inflorescences is limited to branches of more or less long main shoots

FIGURE 78. *Myrtaceae*.—I. *Verticordia pholidophylla*.—II. *V. spicata*; flowering branches. The apex of the inflorescence axis has returned to vegetative growth. (I. W. Australia: Watheroo, Meebold 6619 (M); II. W. Australia, F. Mueller s.n. (M).) III, IV. *Micromyrtus microphylla*.—III. Flowering branching system.—IV. Headlike condensed inflorescence with beginning proliferation (L. Boorman in 9.1908, New South Wales, Australia; M).

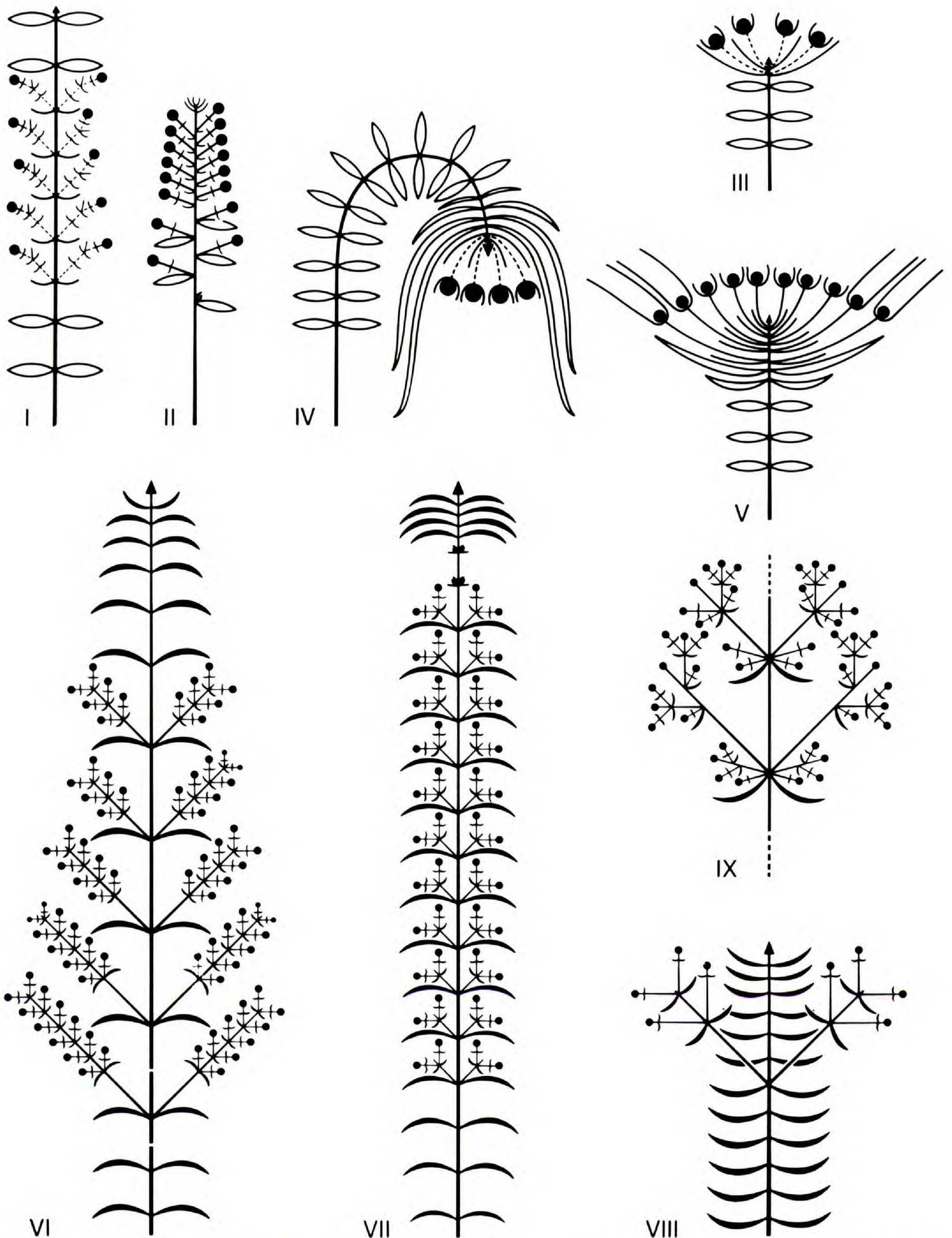


FIGURE 80. *Myrtaceae*. Inflorescence diagrams.—I. *Melaleuca exarata*.—II. *Agonis juniperina* (W. Australia: Albany, A. Meebold 10140, (M)).—III. *Darwinia* with petaloid pherophylls (e.g., *D. virescens*).—IV. *D. meeboldii*.—V. *Actinodium cunninghamii*.—VI. *Chamaelaucium gracile* (E. Pritzel 638); two pairs of *paracladia* omitted.—VII. *Hypocalymma angustifolium* (Weberling 7011c); the hypopodia of the two flowering branches remain undeveloped.—VIII. *Chamaelaucium uncinatum*.—IX. *Myrceugenia exsucca* (paratype: Martius; M). (I, III–V from Briggs & Johnson.)



FIGURE 81. *Myrtaceae*. *Darwinia vestita*. (Left, Pritzel 11/1901; right, Meebold 1216 (M).)

that remain vegetative themselves. This applies to *Baeckea astartoides* Benth., *B. behrii* F. Muell., and others. The next step in this differentiation of a system of vegetative long shoots and flower-bearing short shoots may be that the short shoots develop and flower in the season that follows the development of the long shoot. This was observed in *Campanesia xanthocarpa* Berg, in which the flower-producing short shoots bear cataphylls at their bases (also seen in *Myricariopsis baporetii* (Legrand) Kausel?; see Kausel, 1955–1957: 508, fig. 10). This characteristic “cauliflorous” position of the thyrsoid bracteose inflorescences in *Myrrhinium* species may be explained by an extreme delay of the development and flowering of such short shoots (cf. Fig. 83).

A remarkable reduction of flower-bearing lateral shoots can be observed in some species of *Chamelaucium* and *Hypocalymma*. In *C. uncinatum* Schau. (Fig. 79 II) leafy axes bear pairs of flowering branches that after the production of only two flowers terminate in a bud. This means that only the prophylls of the flowering branches are fertile. Sometimes, however, we can find the flowering branches producing two pairs of flowers before ending in a terminal bud (Fig. 80 VIII). By this observation we are justified to interpret the flower pairs as reduced (commonly anauxotelic) botrytic paracladia, especially as there are species of *Chamelaucium* with botrytic though bracteose flowering shoots (e.g., *C. gracile*, Fig. 80 VI). Whereas in the flowering shoots of *C. uncinatum* the hypopods of first



FIGURE 82. *Myrtaceae*.—*Left*. *Darwinia meissneri* (Meebold 1361 (M)).—*Right*. *Actinodium cunninghamii* Schau. (Meebold 1313 (M)).

and second order are well developed, they are completely reduced in the species of *Hypocalymma* (Fig. 80 VII). Thus the inflorescences of this genus consist of axillary sessile flower pairs including between the flowers a terminal bud that sometimes may become auxotelic. The same inflorescence structure was seen in *Myrceugenia campestris* (DC.) Legrand & Kausel. According to Briggs & Johnson (1979), even the uniflorous elements composing the spikelike inflorescences of *Melaleuca exarata* are lateral flowers of reduced lateral spikes. Except this single lateral flower, which according to Briggs & Johnson must be regarded as terminating a lateral axis of second order, we could only detect a series of about six bracts interpretable as the last remnant of the reduced spikes. In *N. nosophila* F. Muell. the dense spikelike inflorescence, which often proliferates, is composed

of three-flowered cymes (Leins, 1965). A case similar to *Chamaelaucium* can be found in *Rhodomyrtus tomentosa* (Ait.) Wight (Fig. 71 VIII) and *R. parviflora* Alston, and in *Octamyrtus*. Here the prophylls of the flowering branches bear single flowers or triads, and the terminal bud at least produces one pair of small leaves.

Considering the indefinite character of the thyrsic or botrytic inflorescence axes and their main branches, which can be observed in some inflorescences, the question arises whether all of these inflorescences still may be classified as variants of the monotelic type. In many cases the answer is not simple, because the proliferation of various axes within the inflorescence may obscure the true morphological character.

In the thyrsoid paniculate inflorescences of *Syzygium* and many others mentioned above,

there is no doubt about their monotelic character, even if the main axis of these inflorescences terminates in an anauxotelic or auxotelic bud. The same applies to the inflorescence of *Syzygium paniculatum*, which normally is a botryoid (Fig. 68 II) terminating a leafy shoot. The inflorescence of *S. jambos* (L.) Alston differs from these by the abortion of the terminal flower (Fig. 67). Troll (1969: 259) classified this inflorescence as a truncate monotelic synflorescence. Keeping in mind the flexibility in the formation of terminal flowers closing thyrsoid-paniculate inflorescences, which was demonstrated for several taxa of Myrtaceae, this view seems to be acceptable. Commonly the thyrsoid- or paniculate-like flower-bearing branches—the paracladia—of such truncate monotelic systems are still provided with terminal flowers, revealing the monotelic character of the flowering system. Within *Eugenia*, one species with terminal flowers, *E. apiculata* DC. (Fig. 84 VI) was found by Sell (1982), but most of the species seem to have indeterminate flowering systems. The inflorescence structure depicted in Figure 84 I and II is not uncommon: the inflorescence axis terminates in an indefinite botrytic flowering system, and the branches inserted below this terminal botrys repeat this structure. Thus in all essential features this flowering system is in accordance with inflorescences of the polytelic type (Fig. 3 II) as characterized by Troll. According to Troll (1964–1969) and Weberling (1961, 1964, 1965, 1981, 1982, 1983a, b; Troll & Weberling, 1966), the polytelic type probably has been derived repeatedly from the monotelic during the evolution of the different groups of angiosperms by reduction of the terminal flower(s) and specialization of the paracladia of the monotelic system. As a result of this specialization the distal elements of the series of flower-bearing branches are reduced to single lateral flowers or lateral cymes (partial florescences, pf), which constitute elements of an apical system composed of lateral flowers only to which the term “florescence” is referred. The lower lateral branches repeat the structure of the main



FIGURE 83. *Myrtaceae*. *Myrrhinium loranthoides*; flowering branch (I), flower (II), and fruit (III). (From Digilio & Legname.)

stem by producing (indefinite) florescences themselves, co-florescences, and thus are termed paracladia (pc) of the polytelic system (not to be mixed up with the paracladia of the monotelic systems).

Referring this typology to the inflorescences of *Eugenia polystachya* Rich. and *E. muricata* DC. (Fig. 84 I, II), we can regard the terminal botrys as the main florescence and the lateral axes with botrya as paracladia with co-florescences. In the same way the inflorescences of *E. patens* Poir. and several other species can be interpreted; rarely the single lateral flowers are replaced by triadic partial florescences (e.g., *E. muricata*, and according to Briggs & Johnson, 1979: 200, *E. dichotoma* DC.).

These polytelic forms of inflorescences can be derived from monotelic forms as repre-

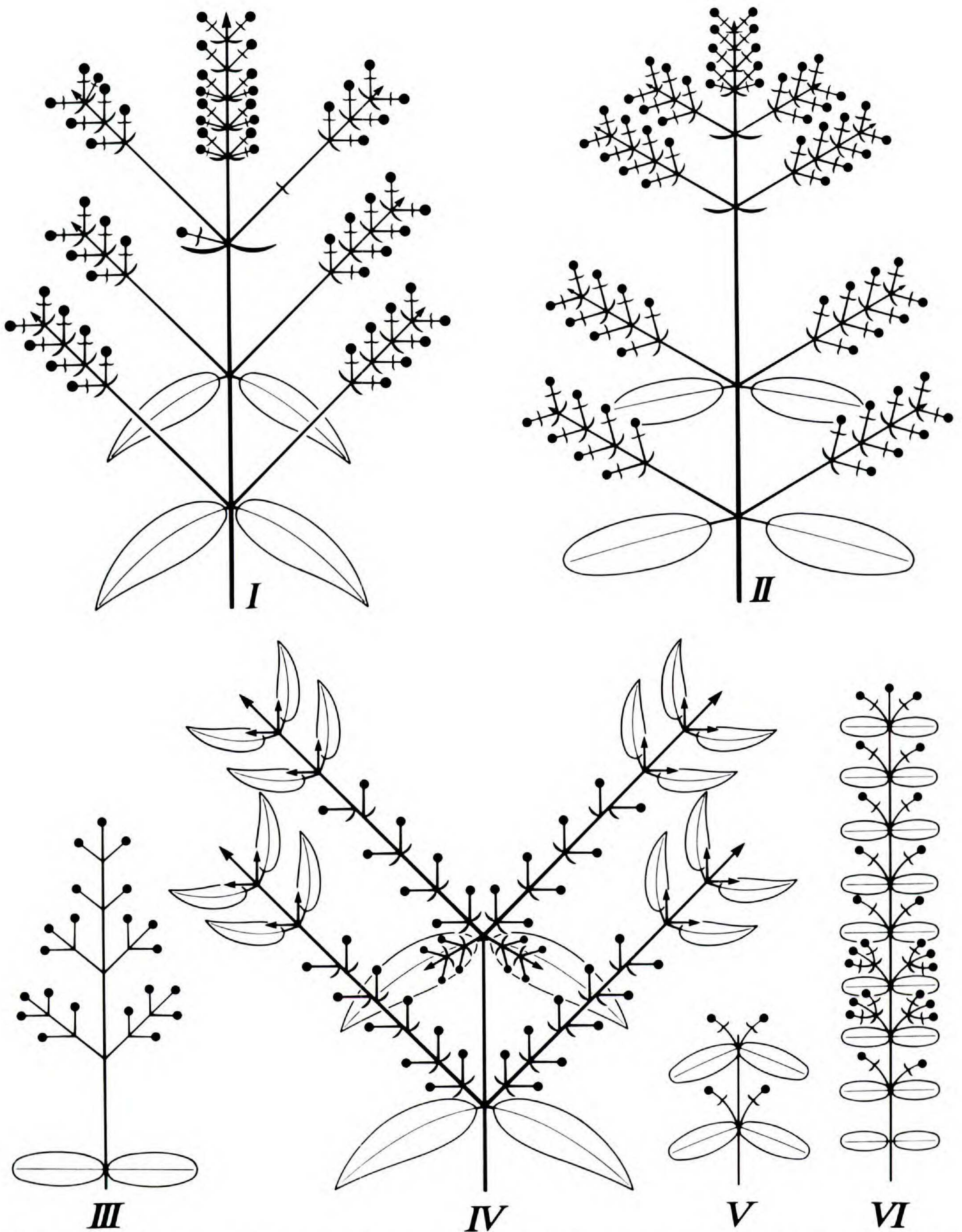


FIGURE 84. *Myrtaceae*. Diagrams of flowering branches.—I. *Eugenia polystachya* (J. M. Pires et al. 50523 (M)).—II. *Eugenia muricata* (Oldeman 2539).—III. *Syzygium aromaticum* (Oldemann B. 1096).—IV. *Eugenia cf. uruguayensis* (Weberling 5577).—V. *E. sancta* (redrawn from *Fl. Mart.* XIV, 2: 26).—VI. *E. apiculata*. (II, III, V from Cremers, 1983/1986; VI from Sell, 1982.)

sented even within *Eugenia* by species like *E. apiculata*. As mentioned before, this species has a thyrsoid-botryoid inflorescence that is still closed by a terminal flower. On the other hand, the pherophylls in this inflorescence are somewhat foliaceous. The same applies to *E. sancta* DC. (Fig. 84 V), with indefinite inflorescences.

In *Eugenia polystachya* the botrytic flowering systems end in a seemingly abortive bud. In others, however, such as *E. cf. uruguayensis* Cambess., they are auxotelic and produce a vegetative continuation of the bracteose botrytic axis (Fig. 84 IV). Proliferation also takes place in the botrytic leafy inflorescences of *E. parviflora* DC. (Sell, 1982) similar to the botrytic leafy proliferating inflorescences of many myrtoid and leptospermoid taxa mentioned above.

In general, a clear tendency towards the polytelic inflorescence structure can be confirmed for the Myrtaceae. In some transitional cases, however, and especially in cases of proliferating inflorescences, it can be difficult to decide whether the inflorescence of a certain taxon should be regarded as a (truncate) monotelic or a polytelic system.

The inflorescences of the Oliniaceae are monotelic throughout and follow the pattern of Myrtaceae with (thyrsoid-)paniculate inflorescences, which we regard to be the central type within the whole order. The panicles are usually conical, caused by shortening of the internodes, but they can be contracted to somewhat globose heads, e.g., in *Olinia rochetiana* A. Juss. The ramification of the branches sometimes tends to be botryoidlike. In some species terminal as well as axillary panicles can be observed. This may be due to the considerably extended and sometimes irregular flowering season (Phillips, 1926): the lowermost paniclelike branches develop separately from the terminal panicle in a somewhat later stage of the flowering season, forming separate flowering systems.

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